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DEVELOPMENTAL ANATOMY OF SEEDLING OF JATROPHA CORDATA[1]

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The anatomical literature of the Euphorbiaceae is well summarized, up to 1902, by Gaucher (5) and, up to 1908, by Solereder (16). The more important papers which have appeared since 1908 include the work of Reiche (12), Swingle (19), Ferry (4), Helm (7, 8), Santos (14), Milanez (10), and Scott (15). Anatomical research done on the roots and stems of Euphorbes, reported in this literature, is principally concerned with the formation of laticiferous, tanniferous, and resiniferous cells or tubes; crystalliferous and granular cell inclusions; cork; collenchyma; fibers and sclerified cells; trichomes; and wood structure. Many problems, including the anatomy of the hypocotyl, studies on the time and place of tissue origin, and direction of tissue differentiation have been neglected. Apparently no one has investigated the entire stem, hypocotyl, and root anatomy of any species of the Euphorbiaceae.

MATERIAL AND METHODS

Jatropha is a large genus of the Euphorbiaceae closely related to *Hevea*, *Manihot*, and *Ricinus* (17) and is composed of about 150 species of trees, shrubs, and herbs. Its distribution is mostly tropical and subtropical in both hemispheres. In North America, *Jatropha cordata* (Orteg.) Muell. is found in Mexico on both sides of the Gulf of California, in the mountains of Baja California, and through Sonora, southern Chihauhau, and Sinaloa to Jalisco. When mature, this species has the growth form of a small tree 20–25 feet high with the superficial appearance of a shrub. A stem of this semi-woody plant 5 inches in diameter can easily be cut in two with one forceful slash of a machete.

Work was begun on the problem in the summer of 1939 at the Desert Laboratory of the Carnegie Institution of Washington at Tucson, Arizona. Seeds, collected near Hermosillo, Sonora, Mexico, were planted one-half inch below the soil level in pots in the greenhouse of the Desert Laboratory. Mature embryos, as well as seedlings of various ages (4, 7, 21, 41, and 75 days old), were preserved in Stover's fluid (3 cc. formalin, 30 cc. ethyl alcohol (95%), 67 cc. distilled water). During the summer, serial sections of the root, hypocotyl, and stem were cut and stained according to a safranin and fast green schedule modified from Johansen's (9).

GENERAL OBSERVATIONS

The root system of the seedling consists of one primary and four adventitious roots, all five of which are similar in size, anatomy, relative position, and time of origin. The primary root differentiates directly downward from the lower end of the hypocotyl. The four procambial strands of the hypocotyl coalesce about

[1]Papers from the Department of Botany, The Ohio State University, No. 443.

50 μ above the collet, resulting in a core of pith and a cylinder of procambium which is continuous from the hypocotyl through the primary root. The four adventitious root primordia originate at the angles of an imaginary square, the corners of which are the points of junction of the four provascular strands of the hypocotyl.

During the first day or two after planting the seed, the adventitious roots remain imbedded in the cortex of the enlarged hypocotyl base (fig. 5). On the third day they push through the epidermis, and by the fourth day the adventitious roots and the primary root are all about 18 mm. long and equal in diameter. From this time on the five roots enlarge and elongate at about the same rate and are comparable in structure. The initiation of secondary roots does not occur until about the seventh day. These may appear first along the lower half of the five principal roots or nearer the base of the hypocotyl.

The straight hypocotyl of the embryo is about 2 mm. long. By the end of the fourth day after planting, when the cotyledons and endosperm emerge from the seed coat, the hypocotyl is about 18 mm. long. On the seventh day it reaches a maximum length of 10–13 cm., at which time the green cotyledons are free from the endosperm in which they were imbedded. The cotyledons bear the same relationship to the endosperm as in *Ricinus communis*. From the seventh day until the plant is two and one-half months old, the hypocotyl continues enlarging, especially at the basal end.

The hypocotyl of *Jatropha cordata* should not be considered a portion of the stem containing the transition region, but rather an organ of the plant possessing a developmental anatomy peculiar to it alone. In the stem-hypocotyl transition, the many leaf traces anastomose, forming four "synthetic bundles"[2] which alternate with the four cotyledon traces. In the upper one-half inch of the hypocotyl, the synthetic bundles anastomose with the cotyledon traces, resulting in four vascular bundles which extend through the organ (fig. 12) to within about 2 mm. of its base, where they coalesce.

The plumule is composed of one node, about 10 μ long, and the apical meristem which extends about 5 μ beyond it. No procambial strands are discernible. During the first four days, the stem elongates to about 120 μ and is composed of two nodes and the meristem which extends about 5 μ beyond the second node. One central and two lateral procambial strands become differentiated in each of the leaf primordia.

By the end of the first week, the stem is about 1 mm. long and six leaf primordia have become organized. The oldest primordium gradually becomes isolated from the five lying above it and from the cotyledonary node by the elongation of adjacent internodes. One new leaf primordium becomes differentiated each week until the plant is four months old or older. Consistently, the apical meristem extends 10 μ beyond the five youngest leaf primordia which remain closely aggregated in the first millimeter of the stem tip. As each successive primordium is organized, the oldest one becomes separated from the five above it by elongation of the intervening internode.

The procambium, which becomes organized some time within the first four days, is distinguishable as a complete ring of meristematic cells at the youngest node of the stem tip. The arc of procambial tissue extending down from the youngest leaf primordium makes up one-half the ring. Three provascular strands are observable in this arc as groups of smaller cells. The remainder of the procambial ring consists of an arc of small meristematic cells similar to and continuous with those of the apical meristem. At the time of differentiation, the cells of the ring show no radial seriation.

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[2]As used by Priestley (11), a synthetic bundle is one "formed by the coalescence of the downward extension of the bundles from higher leaves."

Although there is some variation, especially in the first few internodes, most of the vascular bundles appear to extend through five internodes before anastomosing with other bundles.

In figures 1–4 the general pattern of growth by tissues in the root, hypocotyl, and stem has been recorded. From these graphs it may be inferred that the growth pattern is different for each of the three organs. A comparison of figures 2 and 3 indicates that the growth pattern is similar throughout the hypocotyl, except that growth is more than twice as rapid in the basal as in the upper end. An accurate interpretation of these graphs is dependent upon a knowledge of changes occurring in the various growing tissues. These observations are recorded in the following pages.

EPIDERMIS

The epidermis of the embryo is differentiated from a point about 370 μ from the root apex, through the hypocotyl, to within 10 μ of the stem apex. The thin-walled cells, dense with cytoplasm and radially elongated, divide only anticlinally. During the first four days the epidermal cells of the hypocotyl and most of the root vacuolate, elongate, and enlarge in the tangential direction. Concomitantly anticlinal divisions become less frequent. Cells of the hypocotyl frequently increase in length 4–6 times and double in cross sectional area. The same events occur in the stem as each successive internode elongates.

Ephemeral root hairs differentiate during the second or third day, about 9 mm. from the root apex. The nucleus frequently migrates into these protrusions, some of which become 225 μ long. By the end of the fourth day, many of these first-formed root hairs collapse and begin disintegrating.

A very thin cuticle covers the hypocotyl and plumule of the embryo. By the sixth week it forms a layer which varies in thickness from 1 μ at the stem tip and at the base of the hypocotyl to 6 μ in the mid portions of the shoot. At the same time that the cuticle is being formed, secondary epidermal cell walls form and become 1 μ thick by the middle of the third month.

Stomates differentiate in the epidermis of the embryo covering the basal third of the hypocotyl, and by the end of the third week they are present throughout the lower three-fourths of the epidermal cylinder. No stomates were observed in the epidermis of either the stem or the roots.

Sometime between the first and third weeks, the epidermis and some of the underlying layers of phellem begin splitting longitudinally in places throughout the lower 7 cm. of the hypocotyl. These breaks deepen and lengthen through the remainder of the hypocotyl, root, and stem as the organs increase in diameter. In the portions of the root one month old or older, the epidermis, hypodermis, cortical parenchyma, and outer layers of phellem have split (fig. 11). The crushed and disintegrating epidermal cells lie in broken sheets adhering to the ridges of bark. Sometime after the sixth week, the epidermis and the underlying layers of cork at the base of the stem begin splitting (fig. 13).

HYPODERMIS

The hypodermis of the embryo hypocotyl can be distinguished from the cortical parenchyma on the basis of the cell size, shape, contents, and staining properties but it does not differentiate in the root and plumule until about the fourth day. From that time on it is distinct throughout the plant from a point 10 μ from the stem apex to within 370 μ of the root apex. Although the tissue consists mostly of one layer of square or radially elongated cells, occasionally two and rarely more layers were observed in older roots.

Cessation of rapid anticlinal divisions soon after differentiation is followed by a three-day period of rapid vacuolation and tangential enlargement during which time the cells often triple in length.

In the root, during the first four days, the walls adjacent to the epidermis, the outer portion of the radial walls, and the collenchymatous thickenings which form between the epidermis and hypodermis undergo a chemical change, staining red with safranin. By the end of the first week the entire radial walls of many cells stain red. Collenchymatous thickenings begin forming in the intercellular spaces along the hypodermis-cortical parenchyma junction soon after the first week.

About the fourth day, periclinial divisions initiate a cork cambium in the hypodermis at the base of the hypocotyl. By the third week the cambium is present throughout the hypocotyl (fig. 12); after this time differentiation proceeds slowly, acropetally into the stem. When the plant is two and one-half months old, the hypodermis is uniseriate in the upper half of the stem while in the lower half there is one additional layer of periderm in each successively lower internode. At the collet there are eight layers and at the base of the hypocotyl, twelve layers. The rectangular, tangentially elongated cells of the periderm lie tightly compacted in radial seriation. Secondary cellulose walls, about 1 μ thick, are deposited inside the suberized primary walls of the phellem. The thin-walled cells of the phellogen are similar to those of the phellem in tangential dimension but only half as great in radial dimension. The phelloderm, which represents the enlarged centrad half of the original layer of hypodermis, is composed of one layer of cells comparable in size and vacuolation to those of the phellem but with thin, cellulose primary walls. After phellogen initiation, the cells of the phellogen and phelloderm slowly increase in tangential dimension except in the basal inch of the hypocotyl where the process is very rapid. When the cells are about double their original tangential dimension, they divide anticlinally. Consequently anticlinal divisions are most numerous in the basal inch of the hypocotyl.

CORTICAL PARENCHYMA

The cortical parenchyma of the embryo extends throughout the hypocotyl and to within 320 μ of the root apex. Strictly speaking, the tissue in the root has a definite inner boundary but an approximate outer one, since the endodermis is differentiated in the embryo stage but the hypodermis is not. In the root the number of cell layers (twelve) remain constant until disintegration of the tissue, except in the apical 1 mm. of the primordia where the number has not yet reached twelve. The cells of the eight inner layers are in radial seriation with the actively dividing endodermal cells (fig. 7). Periclinal as well as anticlinal divisions continue longest in those layers nearest the endodermis. Relatively large quantities of starch are present in the cells.

In the hypocotyl, anticlinal and periclinal divisions are restricted to areas adjacent to the phloem for the first 2–3 weeks, after which they spread radially through the cortical parenchyma in the basal inch of the organ and then gradually, acropetally. Divisions are at all times more numerous in the lower inch of the hypocotyl.

During the first week the cells of the cortical parenchyma in the root primordia and hypocotyl undergo tremendous enlargement at which time they lose their decided tangential elongation and become more or less circular in cross section.

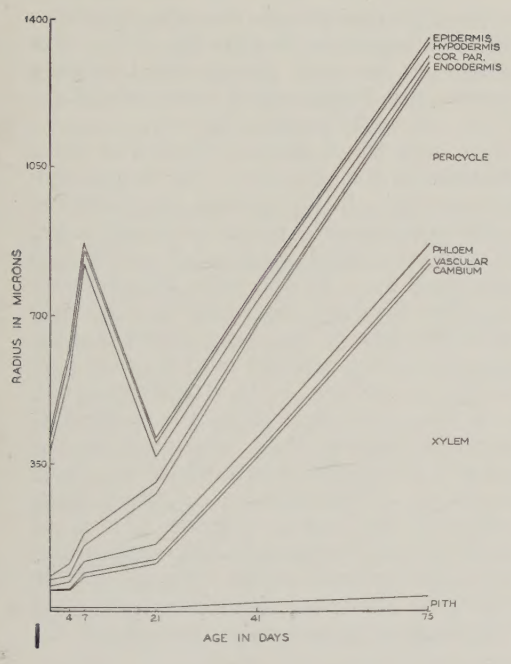
EXPLANATION OF PLATE I

FIG. 1. Graph showing relative widths of the various tissues along the radius during differentiation and maturation in the oldest portion of the root.

FIG. 2. Graph showing relative widths of the various tissues along the radius during differentiation and maturation in the basal end of the hypocotyl.

FIG. 3. Graph showing relative widths of the various tissues along the radius during differentiation and maturation in the top end of the hypocotyl.

FIG. 4. Graph showing relative widths of the various tissues along the radius during differentiation and maturation in the oldest portion of the stem.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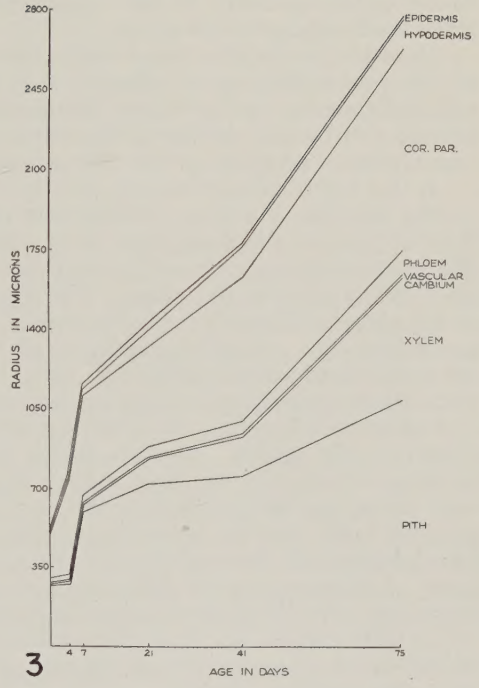
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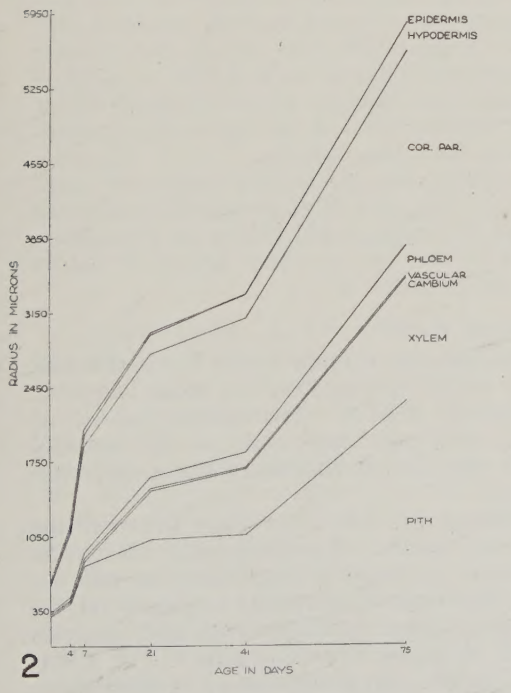
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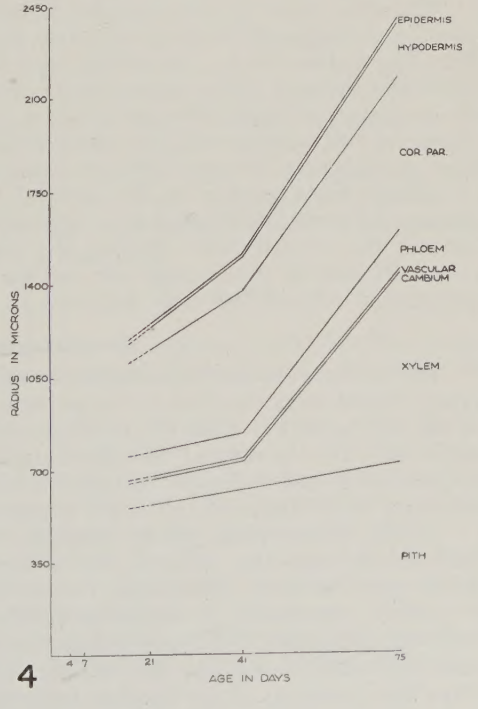
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Many cells, especially in the hypocotyl, increase in cross sectional area 10–15 times and in length 1–4 times.

Between the first and third weeks, the cortical parenchyma in the oldest portions of the root undergoes a collapse, and cell disintegration begins (fig. 10). The radial dimension of the tissue decreases about 80 per cent during this two-week period, and by the middle of the third month only fragmentary remnants of the disintegration products of the protoplasm and cell walls remain (fig. 11).

A few larger, thicker-walled, mostly empty cells which become filled with latex during the first 3–4 days, differentiate adjacent to the phloem in the hypocotyl; they appear in the stem soon after differentiation of the cortical parenchyma. The cortical parenchyma of the stem becomes differentiated at the youngest node, about 10 μ from the stem apex. The small cells are tightly compacted and divide in all planes, although most frequently periclincally. At the time of internode elongation, the cortical parenchyma of the stem becomes distinctly divided into two concentric rings of tissue (fig. 13). Divisions cease in the outer layers of cells, which begin enlarging and elongating tangentially, but centrad to this outer ring and interspersed among the enlarging parenchyma and latex cells, strands of small, dividing cells persist. Similar groups of dividing cells appear in the hypocotyl at about the end of the first week. During the second week, beginning at the base of the hypocotyl and proceeding acropetally, the larger, scattered cells in these strands begin forming secondary cellulose walls. Differentiation of fibers from parenchyma cells proceeds acropetally through the hypocotyl and stem at a rapid rate. Accompanying the differentiation of fibers is an increase in the number and thickness of the laminations deposited inside their primary walls. By the middle of the third month, the secondary walls of fibers in the basal inch of the hypocotyl are about 11 μ thick while in the rest of the hypocotyl and older portions of the stem, they are 7–8 μ thick.

The most recently differentiated fibers in the lower inch of the two and one-half months old hypocotyl are mostly two or more times larger in cross sectional area than any in the shoot. Beginning with the origin of the fiber initials, the enlargement and division of the intervening parenchyma cells results in further separation of the groups of fibers from the phloem. Since the rapidity of cell division and the degree of cell enlargement are greater in the basal inch of the hypocotyl, cortical fiber groups here become farthest separated from the phloem.

Chloroplasts appear in the cortical parenchyma of the hypocotyl and stem during the period of rapid cell enlargement. They are most abundant in the cells nearest the hypodermis. During the week following rapid internode elongation, collenchymatous thickenings are initiated in the two or three layers of tightly compacted cells of the stem adjacent to the hypodermis.

ENDODERMIS OF ROOT[3]

In the embryo, the endodermis forms a cylinder of tangentially elongated cells lying immediately external to the pericycle and extending from the collet to within about 320 μ of the apex of the root primordia (fig. 7). The frequent periclinal divisions and occasional anticlinal ones contribute new cells to the cortical parenchyma and endodermis, respectively (fig. 7). Occasionally the endodermis becomes more than one cell thick in places.

Small, intercellular spaces originate during the first four days between the endodermis and the cells of the adjoining tissues. Simultaneously Casparian strips are initiated. Although the evidence at hand is insufficient to warrant a positive statement, it seems probable that these thickenings originate on the cell walls adjacent to the intercellular spaces between the endodermis and pericycle and gradually move out the radial walls to about the mid-point.[4] For a few days the Casparian strips become more prominent, but in the second or third week,

[3]No endodermis differentiates in either the stem or hypocotyl.

[4]These observations seem to be in accord with the findings of D. S. Van Fleet (20).

when the walls of the endodermal cells undergo a chemical change and stain red with safranin, they lose their identity. Collenchymatous thickenings which stain red with safranin occasionally fill the intercellular spaces adjacent to the endodermis. Beginning about the third week and accompanying disintegration of the cortical parenchyma, the endodermis splits and becomes disorganized (fig. 10). By the middle of the third month it appears fragmentary and mostly crushed to extinction in the ridges of bark.

PERICYCLE OF ROOT[5]

In the embryo root primordia, the pericycle is differentiated to within 320 μ of the apex as a cylinder of cells bounded on the outside by the endodermis and centrad by much smaller cells of the stele (fig. 7). Anticlinal and periclinal divisions in the pericycle contribute cells respectively to a cylinder of pericycle one cell wide and to two strands of small, dividing cells appearing crescent-shape in cross-section. These strands of pericyclic cells lie on each side of the central axis of the diarch root, with the convex arc adjacent to the cylinder of pericyclic cells. (Cf. pericyclic fiber region (PF) in figs. 7, 9, 10.) During the first four days cells nearest the primary xylem points, in the narrowest parts of the strands, begin vacuolating, and some of their walls begin thickening. By the end of the third week all these closely compacted, dividing cells have enlarged and many have differentiated as fibers with thick, laminated secondary walls (fig. 10). Enlargement and division of the parenchymatous cells within the strands, together with pressures exerted by the increasing amount of secondary xylem and phloem, result in a scattering of the pericyclic fibers within the strands and the further separation of the two fiber groups.

During the latter part of the first week the cells of the pericyclic cylinder enlarge slightly in tangential direction, and concomitantly cells opposite the diarch xylem points in the oldest part of the root begin dividing periclinally. From these two original locations, periclinal cell divisions spread tangentially and acropetally through the pericyclic cylinder. By the end of the third week this pericyclic cambium (phellogen) is complete to a point about 400 μ from the root apex (fig. 10). Both phelloderm and phellem are formed, while the phellogen remains as the middle layer (figs. 10, 11). The thin walls of the loosely compacted phelloderm cells are mostly cellulose, while the tightly compacted cells of the phellem have thick, suberized walls. Toward the end of the first week, secondary root primordia are initiated in the pericycle opposite the points of the diarch xylem. All primordia observed were 3.5 mm. or farther back of the root apex.

PHLOEM

Differentiation is very difficult to observe in the phloem, and therefore exact boundaries of this tissue cannot always be accurately determined. Protophloem and metaphloem are indistinguishable.

In the embryo four strands of small, angular, dividing phloem cells extend through the hypocotyl and to within 380 μ of the root apex. In the hypocotyl they lie opposite the four xylem strands while in the root they lie on each side of the xylem points adjacent to the pericycle (fig. 7). Similar primary phloem groups differentiate out of the procambial strands at the fourth node, about 50 μ from the apex. In the root and hypocotyl during the first week and in the stem ar the time of internode elongation, intercalary cell divisions become less frequent and the cells increase in length and cross-sectional area 2–5 times. The most frequent divisions and the most extreme enlargement of cells occurs in the basal inch of the hypocotyl. Soon after cell enlargement, seive tubes, companion cells, and phloem parenchyma differentiate.

Secondary fascicular phloem begins forming in the roots within the first four

[5]No pericycle differentiates in either the stem or the hypocotyl.

days and in the hypocotyl and stem toward the end of the first week. Slow differentiation of secondary interfascicular phloem begins several days following the acropetal differentiation of the interfascicular cambium which is initiated at the base of the hypocotyl during the latter half of the first week. About the second or third week, external to the small portions of secondary vascular cambium, opposite the diarch xylem points in the root, tertiary phloem is initiated. Secondary and tertiary phloem cells are usually larger than those of the primary phloem and lie in radial seriation.

In the second or third week phloem fibers, resembling those of the cortical parenchyma, become differentiated in the basal inch of the hypocotyl. Differentiation proceeds slowly, acropetally through the hypocotyl and into the stem about the end of the second month. They begin differentiating in the root about the middle of the sixth week.

If the cross-sectional area of the companion cells of a 2½ months-old root is arbitrarily used as one unit, the seive tubes are 2½ units in area, the fibers 5.5 units, and the phloem ray cells 11 units.

Owing to the greater number and size of the parenchyma cells lying between the phloem and the fibers of the cortical parenchyma, phloem fibers may be much more readily distinguished in the lower inch of the hypocotyl than in the upper part. In general, phloem fibers are significantly smaller than fibers of the cortical parenchyma.

VASCULAR CAMBIUM

The fascicular cambium of the embryo extends through the hypocotyl only and appears to have differentiated basipetally. These cambial initials elongate tangentially and soon double or triple in that dimension. In the latter half of the first week, concomitant with the elongation of the first internode of the stem and the origin of the phellogen of the hypocotyl and root, (1) fascicular cambia originate at the hypocotyl end of the root, (2) interfascicular cambia originate in the basal end of the hypocotyl, and (3) fascicular cambia originate in the stem.

Differentiation of the fascicular cambium of the stem proceeds basipetally from the third node (about 20 μ) from the stem apex. Cambial cells initiating xylem vessel elements and tracheids are mostly three times greater in tangential dimension than those initiating xylem parenchyma. Immediately following initiation of fascicular cambia, which occurs quickly, parenchyma cells adjacent to the ends of the fascicular cambia divide periclinally and by the time internode elongation is complete, the tangential extension of the interfascicular cambia is complete. Differentiation proceeds acropetally.

After the initiation of the interfascicular cambia at the ends of the fascicular cambia in the base of the hypocotyl, differentiation proceeds laterally and acropetally. By the second or third week the vascular cambium forms a ring in the basal inch of the hypocotyl and by the sixth week it has become a cylinder extending the length of the organ. The vascular cambium continues to be more active in the basal inch than elsewhere in the hypocotyl.

The interfascicular cambial initials in the stem and the basal inch of the hypocotyl increase in size very rapidly but upon becoming twice or three times as great in tangential dimension as the fascicular cambial cells, they divide anticlinally.

EXPLANATION OF ABBREVIATIONS

Used in Figures 7, 9, 10 and 11

(EP, epidermis; H, hypodermis; CO, cortex; EN, endodermis; PER, pericycle; PC, phellogen originating from the pericycle; PF, pericycle fibers or profiber strands; PH, phloem; CA, vascular cambium; CA_2, secondary vascular cambium; SX, secondary xylem; TX, tertiary xylem; XR, xylem differentiated from phelloderm cells formed by the pericyclic (cork) cambium.)

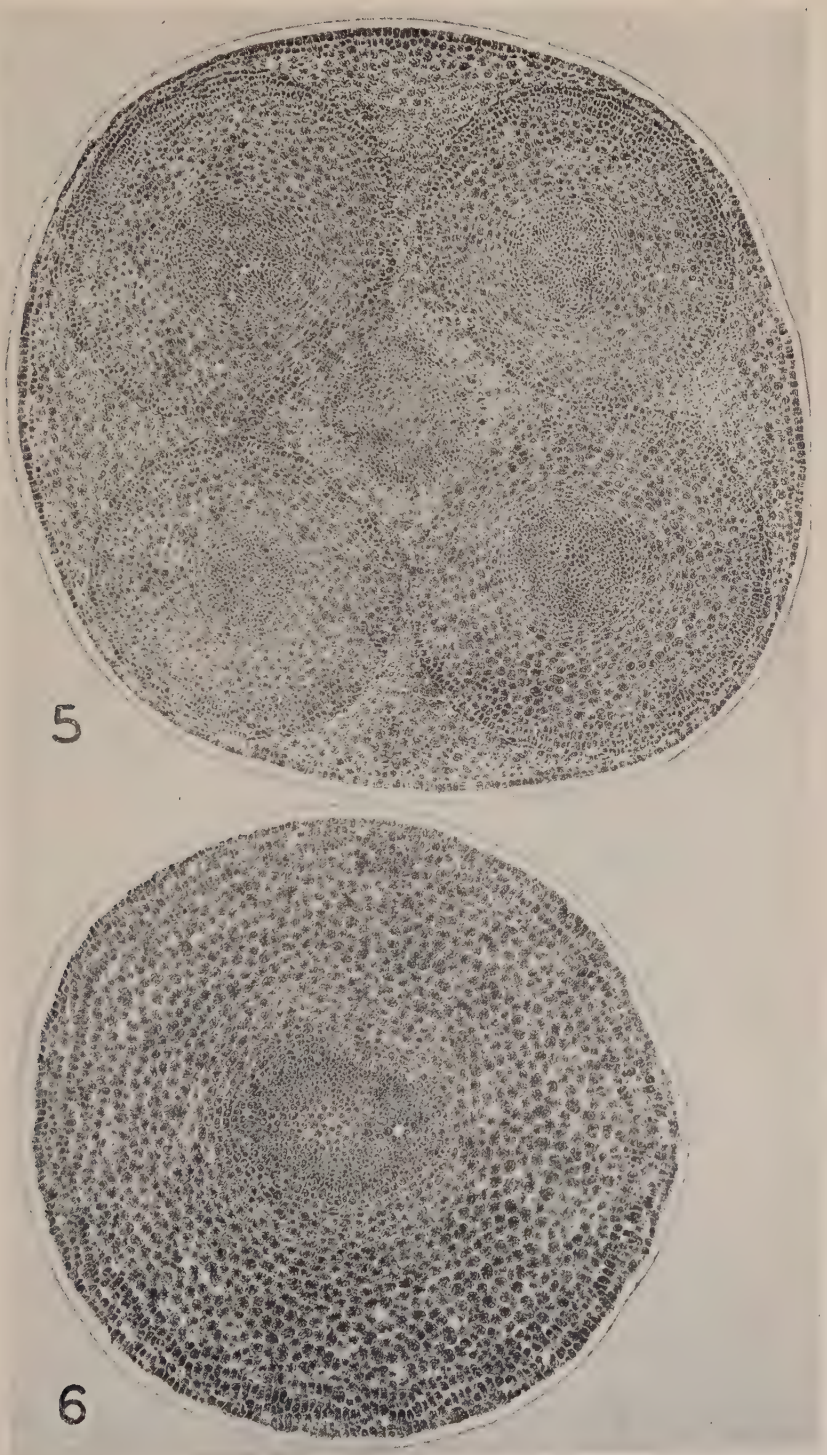

FIG. 5. Cross-section through the basal end of an embryo hypocotyl with cross-sections of a primary and four adventitious roots. × 94

FIG. 6. Cross section through the oldest portion of an embryo primary root. × 45

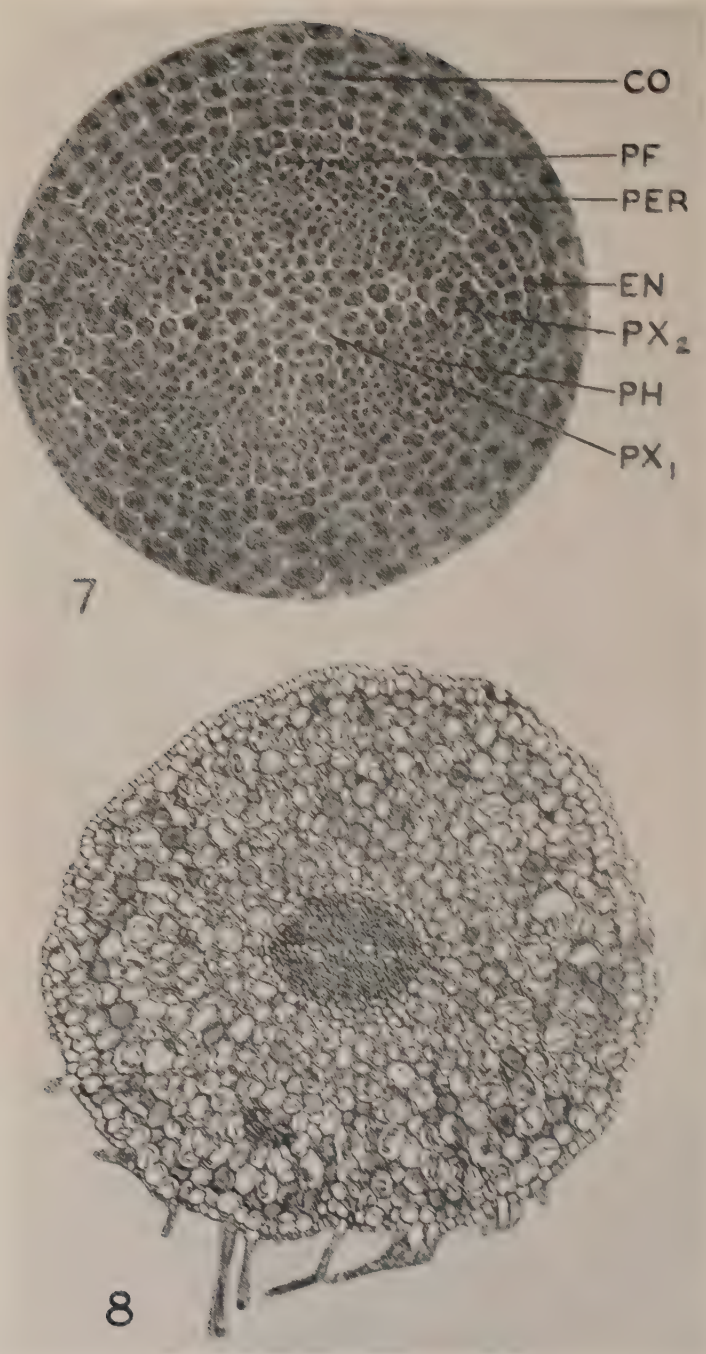

FIG. 7. Cross-section through the central part of the oldest portion of an embryo primary root. × 205

FIG. 8. Cross-section through the oldest portion of a root four days old. × 110

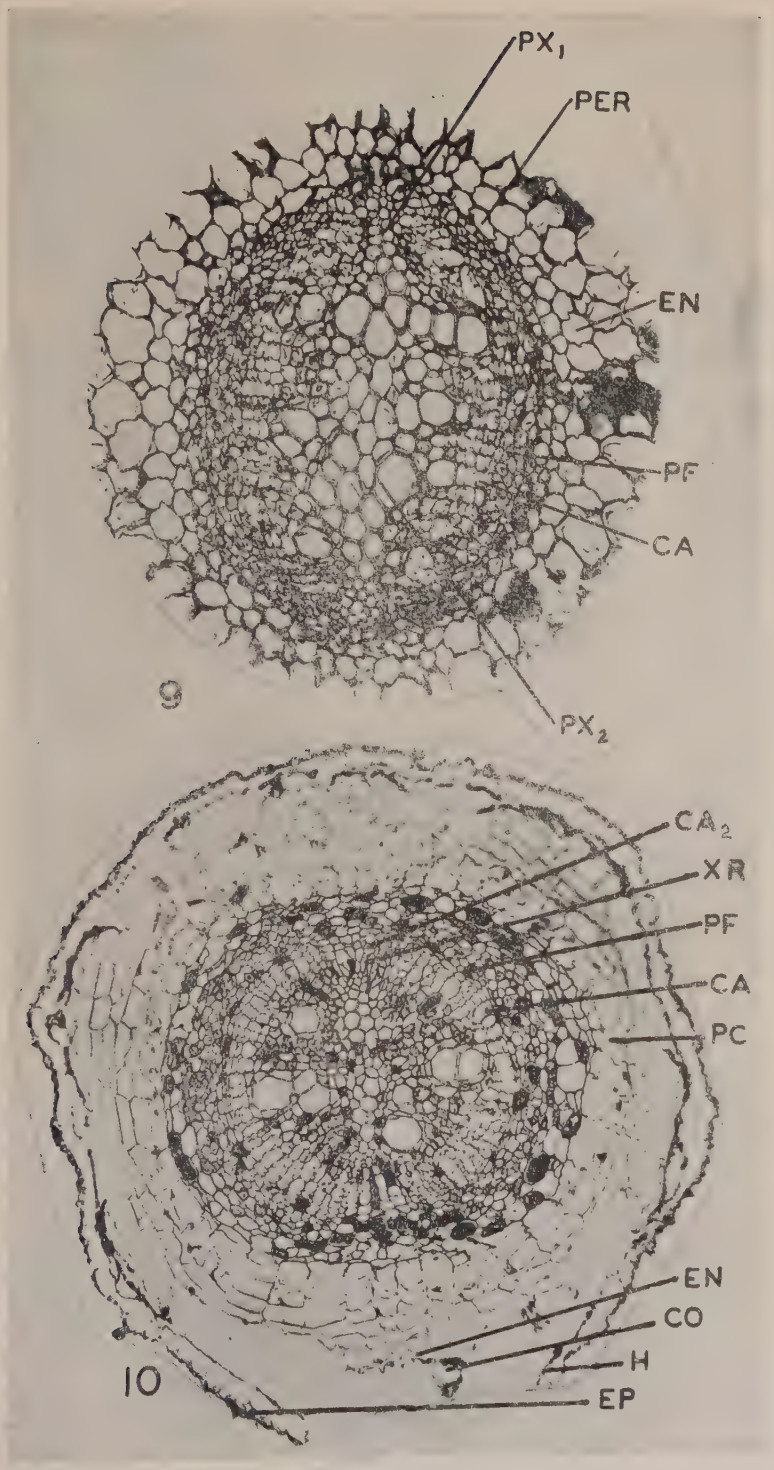

FIG. 9. Cross-section through the central part of the oldest portion of a root seven days old. × 175

FIG. 10. Cross-section through the oldest portion of a root three weeks old. × 121

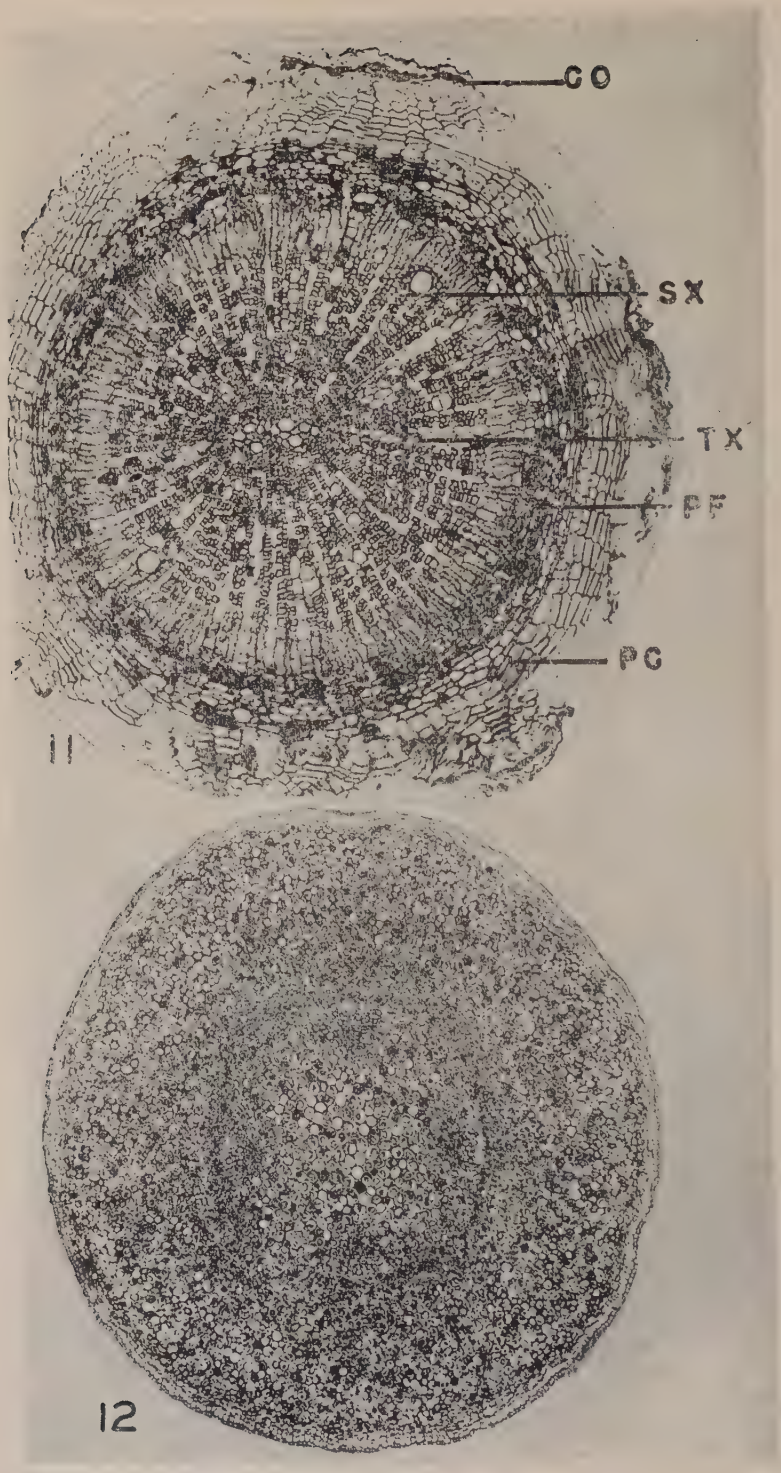

FIG. 11. Cross-section through the oldest portion of a root two and one-half months old. × 48
FIG. 12. Cross-section through the swollen basal end of a hypocotyl seven days old. × 21

The vacuolated initials in the root first appear in four positions along each side of the diarch xylem points but separated from them by xylem parenchyma. The formation of cambial initials proceeds laterally and acropetally until about the end of the first week when the primary vascular cambium is composed of two sheets of cells lying in arcs on each side of the xylem axis (fig. 9). By the end of the third week, and from that time on, they extend to within 1.6 mm. of the root apex. As the xylem increases in bulk, the tangential dimension of the cambial cells doubles or triples. Those initiating xylem or phloem ray parenchyma cells become twice as great in radial and tangential dimensions as other cambial cells. Anticlinal divisions are few.

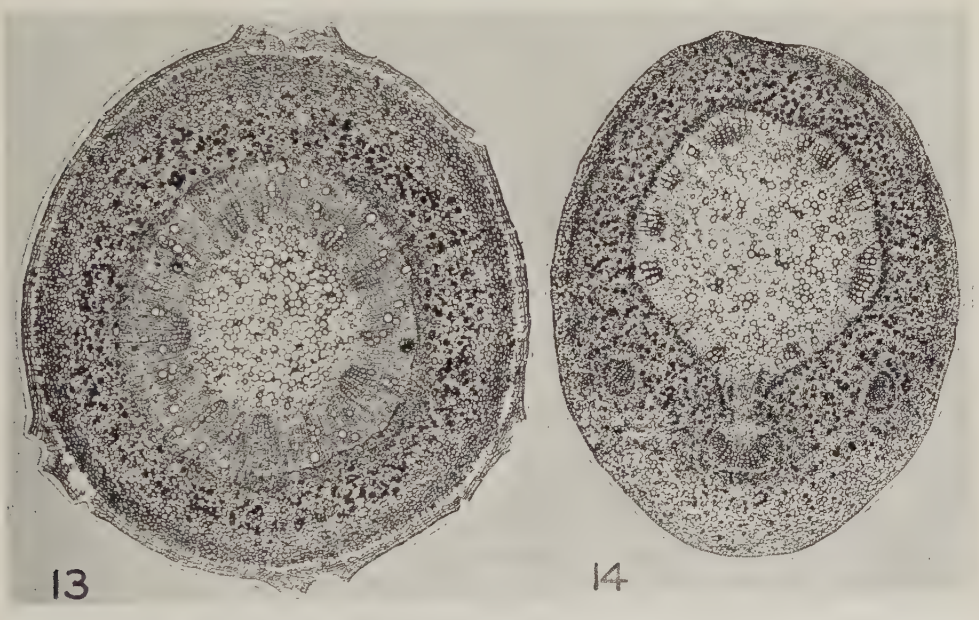

Fig. 13. Cross-section taken immediately above the second node of a stem two and one-half months old. × 23

Fig. 14. Cross-section taken immediately below the seventh node of a stem two and one-half months old. ×17

Most of the secondary tissue which originates from the vascular cambium is xylem (fig. 9), and although the amount of it becomes constantly greater on each side of the central axis, none is formed opposite the xylem points because the vascular cambium has not yet differentiated there (fig. 9). These gaps in the xylem, fan-shaped in cross-section and opposite the diarch xylem points, are in the meantime being filled with phalloderm cells originating from the pericyclic (cork) cambium. The cells are slightly larger than those of the xylem, and many of them are tangentially elongated. Soon after these wedge-shaped groups of phelloderm cells originate, the vascular cambium begins differentiating across them at the hypocotyl end of the root (fig. 10). The differentiation of these secondary portions of the cambial cylinder proceeds so slowly, acropetally, that by the end of the third month they are found only through the upper one-fifth (3 cm.) of the root. The six or seven layers of phelloderm lying centrad of the newly differentiated secondary portions of the vascular cambium become differentiated as xylem (fig. 10).

Sometime after the sixth week, external to the secondary portions of the vascular cambium, phloem becomes differentiated from phelloderm cells, and very soon pericyclic fibers differentiate external to the phloem. In the oldest portion of a 2½ month-old root, the pericyclic fibers form a complete cylinder (fig. 11).

XYLEM

Primary xylem is present in the root but is never found either in the stem or in the hypocotyl, with one minor exception.

A primary diarch xylem is defined in the steles of the embryo root primordia to within 310 μ of the apex, on the basis of cell size and position (figs. 6, 7). The xylem cells nearest the center of the root stop dividing and become greatly enlarged before divisions cease in the cells nearest the pericycle (fig. 7). The first xylem cells to differentiate, therefore, are those larger elements located nearest the center of the root. Within the first day or so, proliferation ceases in the small xylem cells adjacent to the pericycle. Differentiation proceeds from the hypocotyl end of the root to within 1,000 μ of the apex. Lignification and maturation of these cells begins the next day following differentiation and progress rapidly acropetally but rather slowly centripetally. By the end of the fourth day approximately thirty of the elements nearest the pericycle at the hypocotyl end of the root have spiral or annular lignified secondary walls (fig. 8). It is not until about the end of the first week that secondary wall formation and lignification begins in those cells nearest the center of the root. The lignified walls of these cells, which frequently become 3 μ thick, are reticulate or occasionally pitted.

Simultaneous with the formation of the two arcs of vascular cambium, xylem fibers become differentiated from primary cells on opposite sides of the diarch xylem axis. The xylem fibers are similar to the pericyclic and phloem fibers, except that on the average they are two or three times larger in cross-sectional area. Their secondary walls are slightly lignified, often becoming 3 μ thick but they frequently contain cytoplasm and nuclei. Differentiation of fibers from primary and then from secondary xylem parenchyma proceeds rapidly, centrifugally, on both sides of the lignified xylem axis (figs. 8, 9, 10, 11). Differentiation and lignification of additional vessel elements scattered among the fibers occur only occasionally, but those formed are usually extremely large.

When the secondary portions of the vascular cambium differentiate across the wedges of secondary tissue opposite the xylem points (fig. 10), the cells lying centrad of them differentiate as xylem fibers, parenchyma, and lignified elements. Cells initiated centripetally by the secondary portions of cambium become differentiated as tertiary xylem (fig. 11).

Uniseriate or biseriate rays of xylem parenchyma begin differentiating during the fifth or sixth week. These large, thin-walled cells are sometimes crushed by the enlarging elements adjacent to them. In the oldest part of a root 2½ months old, lignified elements, very few of which are located in tertiary tissue, comprise about 10 per cent of the xylem bulk. Xylem parenchyma, most of which lies in xylem rays and close to the cambium, makes up about 20 per cent of the xylem. The remaining 70 per cent consists of fibers (fig. 11). The largest cells of each type are those most recently initiated by the cambium. This is partly due to the gradual increase in size of the vascular cambium initials.

The secondary xylem of the embryo hypocotyl lies in four equally spaced strands which are continuations of the cotyledonary bundles (fig. 12). Each xylem strand contains about five radial rows of enlarged cells which later mature as vessels. Each of the rows is separated by one or more rows of xylem parenchyma. Since there are five vessel initials per row in the basal end of the hypocotyl and six at the top end, it may be inferred that differentiation of the vascular cambium and its secondary xylem proceeded basipetally. Maturation, indicated by lignification of secondary thickenings and disintegration of cell contents, follows quickly,

centrifugally during the first four days. On the third or fourth day the maximum number of vessels per row is reached, there being about eight per row in the basal inch and six per row in the rest of the hypocotyl. In the first lignified vessels the thickenings are annular, and in successively younger elements, stretched spirals, spirals, and tight spirals were observed. Some of the cells of the xylem parenchyma lying between the rows of vessels enlarge greatly and become differentiated as uniseriate, or occasionally biseriate, xylem rays which are perpetuated by divisions of certain cambial cells. Most of the cells differentiate as xylem fibers possessing slightly lignified, cellulose, secondary walls which frequently become 3 μ thick. At this same time, several very small cells with annular, partly lignified thickenings become differentiated from the primary pith parenchyma at the secondary xylem points.

Between the fourth and seventh days xylem cells are initiated by the interfascicular cambium in the basal inch of the hypocotyl and rapidly enlarge until they are nearly comparable in cross-sectional area to the largest vessels. Additional cells are formed as the interfascicular cambium differentiates laterally and acropetally. The first five layers of cells produced before the end of the third week remain parenchymatous. Many of the cells initiated between the third and sixth weeks in the basal end of the hypocotyl differentiate as fibers. Among these are scattered a few vessels whose secondary walls become thick and lignified. Sometimes after the sixth week rays of large parenchyma cells differentiate in the interfascicular xylem.

The secondary xylem of the stem originates at the third node, about 20 μ from the stem apex with the differentiation of one small strand of cells representing the downward extension of the central vascular bundle of the leaf primordium attached at that node. At the time of internode elongation twelve leaf traces are differentiated (fig. 14). In each trace there are about five uniseriate plates of xylem parenchyma alternating with four uniseriate plates of vessels. Vessels continue differentiating until about the sixth week, when the maximum number (five to nine) per radial row has been reached. In the second or third week xylem fibers begin differentiating from newly formed secondary xylem parenchyma, and by the middle of the third month the secondary cellulose walls are 1 μ thick.

Vessel differentiation in the leaf traces is basipetal through the stem, as evidenced by the decrease in vessel number, secondary wall thickness, and secondary wall lignification. Initiation and lignification of vessels occur first in the larger central trace of the leaf, and later in the two lateral traces.

During the second week the interfascicular cambia of the stem begin differentiating acropetally and tangentially from the ends of the fascicular cambia. The first few layers of xylem cells, those lying farthest centrad remain parenchymatous, but most of those cells originating from the interfascicular cambia after the third week differentiate as fibers. Occasional vessels differentiate among the fibers of both the fascicular and interfascicular xylem (fig. 13). Beginning about the sixth week uniseriate rays composed of large parenchymatous cells differentiate throughout the xylem. Occasionally the walls of these cells become slightly thickened.

PITH

Pith is the first tissue of the root to differentiate. Its closely compacted, angular cells extend to within 300 μ of the root apex and form a continuation of the pith of the hypocotyl. The large cells usually remain parenchymatous but occasionally the walls become slightly thickened.

In the embryo hypocotyl the cells are loosely compacted, dense with cytoplasm, and contain much starch, most of which disappears during the third week. Anticlinal and periclinal divisions occur frequently only in the lower end of the hypocotyl. Divisions cease during the first four days but are reinitiated in the

fourth or fifth week. The cells begin enlarging soon after their formation, and by the third week those in the base of the hypocotyl have increased in cross-sectional area more than seven times, those in the upper parts more than two times. Cell elongation occurs concomitantly and is approximately equal in the cells throughout the organ. On about the seventh day a cavity formed by the tearing of cells in the center of the pith originates in the base of the hypocotyl, and by the third week it extends throughout the organ.

Pith becomes differentiated in the stem at about the fourth node, 60 μ from the apex. The cells are closely compacted and contain no starch. Cell divisions occurring in all planes cease at about the time of internode elongation. The cells gradually become rounded as they increase greatly in size.

DRUSES AND LATICIFEROUS CELLS

Large, spherical aggregates of crystals (druses), presumably of calcium oxalate, and appearing yellow in prepared sections, were observed filling isolated cells in many tissues of the plant. They first appear in the cortical parenchyma of the root on about the seventh day; in the tissue lying centrad of the pericyclic (cork) cambium in the second or third week; and in the phloem, especially in the phloem rays, sometime after the sixth week. In the hypocotyl they first appear in the cortical parenchyma and pith between the fourth and seventh days; in the phloem and hypodermis between the first and third weeks; and in the xylem sometime after the sixth week. In the stem they first occur in the hypodermis, cortical parenchyma, phloem, and pith in the second or third week.

Laticiferous cells occur singly, or form short crooked tubes in many tissues of the plant. The contents of these cells stain red with safranin. In the root, laticiferous cells differentiate in the xylem, phloem, and tissue centrad of the pericyclic (cork) cambium, during the second or third week. In the hypocotyl they differentiate in the cortical parenchyma of the embryo; in the phloem during the fifth or sixth day; and in the xylem between the first and third weeks. Both druses and laticiferous cells are more abundant in the basal inch of the hypocotyl than in the upper parts of the organ. In the stem they differentiate among the cells of the meristem in the embryo stage. After tissue differentiation, they are found in the cortical parenchyma. Latex frequently fills the lignified vessels in the stem.

TERMINOLOGY

In this paper, a cell or tissue is considered *differentiated* from a group of cells when it can be distinguished from them on the basis of differences in cell size, shape, contents, rate of cell division, or differences in the cell wall. It has been assumed that the cell or tissue continues differentiating as long as visible[6] changes occur in it.

The term *mature* has been applied to cells which are incapable of further differentiation, that is, dead cells. The writer is aware that cells may become "physiologically mature" long before death but—since it is impossible to determine whether the processes in a cell will undergo considerable change later in life or remain more or less constant—it is impossible to determine when a cell is "physiologically mature."

In recording the observations on xylem, it will be noted that use of the terms *proto-* and *metaxylem* has been avoided. So many misconceptions regarding these terms are at large in the literature that they no longer convey the same meaning to all plant anatomists. It would seem, therefore, that these concepts are in urgent need of re-examination and revision in the light of recent facts.

The terms were proposed by Russow (13) in 1872. As defined by him,

[6]It is understood that physiological differentiation precedes visible differentiation and that it may continue afterward.

protoxylem refers to the first xylem elements to *differentiate*. He states not only that these elements are primary in origin, but that they are the first to become thick walled and hence to mature. He realized, however, that the pattern of the secondary wall is directly related to the degree and speed of cell elongation at the time of secondary wall formation.

DeBary (2) apparently retained the term as defined by Russow but imposed one additional limitation by stating that protoxylem consists of tracheae with spiral or annular thickenings.

According to Coulter, Barnes, and Cowles (1), "The first xylem elements to appear (in the stem) are small in caliber, and of the spiral kind, a kind especially adapted to a region of rapid elongation. These groups of spiral vessels are called the *protoxylem*, and the later vascular elements form the *metaxylem*."

In Eames and MacDaniels (3), "The first cells of the phloem to mature are known as the *protophloem*, those of the xylem, the *protoxylem*." The cells of the protoxylem are further characterized as being primary in origin, narrow and slender, and possessing annular; spiral, or perhaps scalariform secondary walls.

Hayward (6) states that "The primary xylem is further divided into the *protoxylem*, which is the first to differentiate and mature at a given locus, and the *metaxylem*, which usually matures later." Elsewhere he defines protoxylem as "the first elements of primary xylem to be differentiated, characterized by annular, spiral, or reticulate secondary walls."

Priestly and Scott (11) have showed that the xylem of *Helianthus annuus* stem is all secondary in origin. The first xylem elements to differentiate are also the first to mature and possess annular or spiral secondary walls. Those elements differentiating and maturing later are characterized by scalariform, reticulate, and pitted secondary cell walls. In the roots of *Helianthus*, the first xylem formed is primary in origin. These workers offer the suggestion that "It would seem far better to use the terms 'primary' and 'secondary' with their usual implications and to recognize them in the shoot, . . . the protoxylem is usually secondary, being derived from the inner members of the radial series of cells cut off from the cambium." Since protoxylem and metaxylem have in the past connoted primary origin to most of us, it would seem that although this suggested usage of the terms is fundamentally sound, general acceptance and accomplishment of such a change would be a practical impossibility and would only result in further confusion in the literature.

Stover (18) has called attention to the absence of xylem elements with annular or spiral secondary walls in the slow-growing rhizomes of *Agropyron repens*, *Spartina michauxiana*, and *Calamovilfa longifolia*. In the same paper he also reports that in the vascular bundles of rapidly growing young plants of *Zea mays*, all of the xylem vessels possess annular or spiral secondary walls and that these vessels are extremely large. All of the xylem in the species with which Stover worked was primary in origin.

In *Jatropha cordata*, it has been noted that the first xylem cells to differentiate in the stem are also the first to mature. All of the xylem is secondary in origin. In the hypocotyl, the first xylem cells to differentiate are the first to mature. Most of the xylem in the hypocotyl is secondary although a few primary elements may differentiate and mature after a considerable quantity of secondary xylem has matured. The first xylem cells to differentiate in the roots are located in the center of the root and are primary in origin. The last cells of the primary xylem to differentiate (lying nearest the pericycle) are the first cells of the primary xylem to mature. Secondary xylem forms after all of the primary xylem has differentiated and after much of it has matured. The cells of the xylem with annular and spirally thickened secondary walls were always found to be the first cells to mature although these cells were secondary in origin in the stem and hypocotyl and primary in origin in the root.

The data cited above are conclusive evidence that in the differentiation of xylem cells, the size, location, time of enlargement, time of secondary wall lignification, time of differentiation, and the pattern of the secondary wall do not always bear a specific or constant relationship to the kind of origin, whether primary or secondary. In view of the existing confusion, it seems that the most practical solution of the problem is to discard entirely the terms proto- and metaxylem in

TABLE I

DIRECTION, PLACE, AND TIME OF TISSUE DIFFERENTIATION IN THE ROOT, HYPOCOTYL, AND STEM

Tissue	Organ	Direction of Differentiation	Place and/or Time of Differentiation
Epidermis	Root	A	370 μ from root apex; prior to planting
	Hypo.	?	Prior to planting
	Stem	A	10 μ from stem apex, at base of apical meristem; within first 4 days
Hypodermis	Root	A	370 μ from root apex; within first 4 days
	Hypo.	?	Prior to planting
	Stem	A	10 μ from stem apex, at base of apical meristem; within first 4 days
Hypodermal cambium	Root	N	None
	Hypo.	A	Base of hypocotyl; between fourth and seventh days
	Stem	A	Base of stem; between first and third weeks
Cortical parenchyma	Root	A	320 μ from root apex; prior to planting
	Hypo.	?	Prior to planting
	Stem	A	10 μ from stem apex, at base of apical meristem; within first 4 days
Endodermis	Root	A	320 μ from root apex; prior to planting
	Hypo.	N	None
	Stem	N	None
Pericycle	Root	A	320 μ from root apex; prior to planting
	Hypo.	N	None
	Stem	N	None
Pericyclic cambium	Root	A	400 μ from root apex; between fourth and seventh days
	Hypo.	N	None
	Stem	N	None
Primary phloem	Root	A	380 μ from root apex; prior to planting
	Hypo.	?	Prior to planting
	Stem	B (?)	Fourth node below stem apex; after fourth day
Vascular cambium	Root (pri)	A	1600 μ from root apex; within first four days
	Root (sec)	A	At collet; between first and third weeks
	Hypo. (fas)	B (?)	Prior to planting
	Hypo. (int)	A	Base of hypocotyl; between fourth and seventh days
	Stem (fas)	B	20 μ from stem apex, at third node from stem apex; after fourth day
	Stem (int)	A	At internode elongation; after fourth day
Primary xylem	Root	A	310 μ from root apex; prior to planting
	Hypo.	A	Within first 4 days
	Stem	N	None
Pith	Root	A	300 μ from root apex; prior to planting
	Hypo.	?	?
	Stem	A	60 μ from stem apex, at fourth node from stem apex; within first 4 days

A, acropetal; B, basipetal; N, none differentiated; pri, primary tissue; sec., secondary tissue; fas, fascicular; int, interfascicular.

favor of meaningful descriptive phrases such as "the first xylem cells to differentiate," "the first xylem cells to mature," or "the xylem elements with spiral, annular, reticulate, or scalariform thickenings," whichever is applicable to the case at hand. It will, of course, be necessary to make clear whether the cells are primary or secondary in origin.

SUMMARY

1. The time and place of origin of the various tissues of the root, hypocotyl, and stem are summarized in Table I. It is apparent that a high degree of tissue differentiation has already taken place in the root primordia and hypocotyl of the embryo by the time of seed maturity, while very little has occurred in the epicotyl.
2. The relative quantities of the various tissues present at different times during the enlargement of the root, hypocotyl, and stem are summarized in figures 1–4.
3. The order of tissue differentiation in the root is (1) pith, (2) primary xylem nearest the center of the root, (3) pericycle, endodermis, and the inner boundary of the cortical parenchyma, (4) hypodermis and epidermis, (5) primary phloem, (6) primary xylem nearest the pericycle, (7) the primary vascular cambium and secondary xylem and phloem, (8) the pericyclic (cork) cambium, and (9) the portions of secondary cambium and tertiary xylem and phloem.

   The order of tissue differentiation in the hypocotyl is (1) epidermis, hypodermis, cortical parenchyma, primary phloem (both fascicular and interfascicular), primary fascicular cambium, and pith, (2) secondary fascicular xylem, (3) secondary fascicular phloem and primary xylem, (4) primary interfascicular cambium and secondary interfascicular xylem and phloem.

   The order of tissue differentiation in the stem is (1) epidermis, hypodermis, and cortical parenchyma, (2) pith, (3) primary fascicular cambium and secondary xylem, (4) primary phloem, (5) secondary fascicular phloem, (6) primary interfascicular cambium and secondary interfascicular xylem and phloem.
4. The hypocotyl cannot be considered a portion of the stem occupied by the transition region but should be thought of as an organ of the plant possessing a developmental anatomy peculiar to it alone.
5. Elongation of the hypocotyl is due primarily to cell elongation rather than cell division.
6. The phenomena accounting for the extreme enlargement at the base of the hypocotyl are, (a) very little cell elongation accompanies cell enlargement in the base of the hypocotyl while in the upper parts, cell elongation is extreme and accounts for most of cell enlargement, (b) the interfascicular cambium is initiated in the base of the hypocotyl, (c) cambial initials become larger in the base of the hypocotyl and finally divide anticlinally, increasing the total number of cambial cells, (d) reinitiation of intercalary cell divisions throughout the cortex of the hypocotyl commences in the basal end.
7. In the root, a diarch primary xylem is differentiated. The cells nearest the pith differentiate first while the cells nearest the pericycle mature first. In the hypocotyl, an extremely small amount of primary xylem is differentiated after some secondary xylem has formed. No primary xylem is differentiated in the stem.
8. Fibers with thick, cellulose walls comprise more than half of the xylem throughout the mature plant.
9. In the root, during the second or third week, secondary cambia differentiate

across the secondary tissue opposite the xylem points and from it arise tertiary xylem and phloem.

10. Secondary root primordia become initiated in the pericycle opposite the points of the diarch xylem toward the end of the first week.

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OHIO SHALE CONODONTS

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Although conodonts are numerous in the Ohio shale, they have received very little attention. To my knowledge, Cooper's paper (1931a), in which seven species are described from the top of the shale just northeast of Columbus, is the only publication on the subject. The present study encompasses a large variety of species and is the forerunner of a comprehensive study of the conodont fauna.

The material for this paper was collected from the lower portion of the Ohio shale where it is exposed along a few small tributary streams of the Olentangy River about two miles northwest of Worthington, in central Franklin County. Thirty-seven previously described species and eighteen genera are recognized. Twelve forms are unassigned because of doubtful relationships. Among these may be several new species and at least one new genus. It is hoped that these doubtful forms can be described when additional material is collected and studied.

The species described in this paper are listed as follows:

Ancyrognathus irregularis Branson and Mehl

Bryantodus commutatus Huddle
Bryantodus concavus Huddle
Bryantodus germanus Holmes
Bryantodus inequalis Holmes
Bryantodus nitidus Ulrich and Bassler
Bryantodus serrulus Huddle
Bryantodus subcarinatus Huddle
Bryantodus subequalis Cooper
Bryantodus subplanus Huddle

Euprioniodina prona Huddle

Hibbardella angulata (Hinde)
Hindeodella aculeata Huddle
Hindeodella alternata Ulrich and Bassler
Hindeodella germana Holmes
Hindeodella subtilis Ulrich and Bassler
Hindeodella sp. 1
Hindeodella sp. 2

Hindeodelloides bicristatus Huddle

Ligonodina sp. 1
Ligonodina sp. 2
Ligonodina sp. 3

Lonchodina multidens Hibbard
Lonchodina perarcuata Ulrich and Bassler
Lonchodina perlonga Ulrich and Bassler

Metaprioniodus biangulatus Huddle

Ozarkodina delicatula (Stauffer and Plummer)

Palmatodella delicatula Ulrich and Bassler
Palmatodella ? sp.

Palmatolepis glabra Ulrich and Bassler
Palmatolepis quadrantinodosa Branson and Mehl
Palmatolepis regularis Cooper
Palmatolepis subperlobata Branson and Mehl

Polygnathus nodocostata Branson and Mehl
Polygnathus pennatuloidea Holmes
Polygnathus sublatus Ulrich and Bassler
Polygnathus sp.

Prioniodina separans Holmes

Prioniodus alatoides Holmes
Prioniodus alatoideus Cooper
Prioniodus alatus Hinde
Prioniodus cultratus Ulrich and Bassler

Spathognathodus subrectus (Holmes)

Subbryantodus radians Branson and Mehl
Subbryantodus sp.

Synprioniodina sp.

Distacods, 3 sp.

Dermal plates, 2 sp.

No additional evidence is furnished by the present conodont collection to aid in the solution of the general problem of the stratigraphic position of the Ohio shale. It is expected, however, that future studies will reveal data of value in determining the age relationships of the formation.

The conodonts occur most commonly in very thin bone beds in the shale, with only occasional specimens scattered between the beds. Some of these bone beds are located at the contacts between the black shale and interbedded layers of gray shale. Others may be found as very thin layers along bedding planes in black shale of uniform lithology. In most places the conodonts are rather evenly distributed laterally, but in one place at least they are concentrated in small discontinuous patches which consist largely of conodont fragments. This latter occurrence suggests that they were brought together by small eddies or currents in

the water and that they were moved about considerably as they were being deposited, thus resulting in their fragmental condition.

The state of preservation of the conodonts at the different exposures varies in a marked degree. In some places the fossils are largely broken, but the fragments are excellently preserved. In other layers the conodonts have been dissolved away by the sulfuric acid produced by the weathering of pyrite and marcasite in the shale outcrops and have left clearly defined impressions or molds which are usually sufficiently complete to permit identification.

The conodonts are quite variable in color, some being white, some amber-colored and transluscent, and others are colorless and so transparent that the shale on which they lie may be seen through them. Many of the specimens examined have a high luster. In general, the fossils of any one bed are similar in color regardless of the species.

Associated with the conodonts are small dermal plates, minute black spines, small carbonaceous fragments of wood, and a great abundance of plant spore cases which are in some instances so numerous that the surfaces of the shale are almost completely covered with them. In two of the bone beds which were studied a fine network of minute cylindrical tubes was observed. These are filled mostly with pyrite and marcasite crystals, but in places they are hollow. Their identity is unknown.

For the most part the conodonts described in this paper had to be studied in place on the slightly weathered surfaces of the thin layers of shale, because when the rock was broken down the conodonts fell apart along minute fractures. Some fossil material was separated successfully from the shale by boiling in a solution of sodium hydroxide, and the conodonts were recovered by sifting and by using liquid separates. Material thus separated from the shale consisted largely of fragments, but some identifiable specimens of the simple cone type as well as many minute specimens of the platform type were recovered. These will be studied at a later time.

The total number of fossils preserved sufficiently well for study was about 450. This is a rather small number considering that at least thirty-seven species are represented. Branson and Mehl have also noted a proportionately large number of species relative to the specimens examined in their collections from the Harding sandstone of Colorado (1933a, p. 22), and from the Grassy Creek shale of Missouri (1933b, p. 183).

Acknowledgment is made of the assistance of Dr. Grace A. Stewart of the Department of Geology, Ohio State University, who directed the paleontological research.

EXPLANATION OF PLATE I

All specimens are from the lower portion of the Ohio shale, upper Devonian, central Ohio. Magnification as noted.

Figs. 1–3, Distacodidae. Figured specimens: ×50 (p. 23). **4, 6,** *Prioniodus alatoideus* Cooper. Hypotypes: 4, an impression, ×30; 6, × 25 (p. 23). **5, 7,** *Prioniodus alatoides* Holmes. Hypotypes: 7, an impression. ×25 (p. 23). **8,** *Prioniodus cultratus* Ulrich and Bassler. Hypotype: ×25 (p. 23). **9,** *Prioniodus alatus* Hinde. Hypotype: ×20 (p. 23). **10,** *Ligonodina* sp. 1. Figured specimen: an impression. ×12 (p. 23). **11, 12,** *Euprioniodina prona* Huddle. Hypotypes: impressions. ×25 (p. 23). **13,** *Synprioniodina* sp. Figured specimen: an impression. ×20 (p. 23). **14,** *Ligonodina* sp. 2. Figured specimen: an impression. ×10 (p. 23). **15,** *Palmatodella delicatula* Ulrich and Bassler. Hypotype: ×20 (p. 23). **16, 17,** *Hindeodelloides bicristatus* Huddle. Hypotypes: 16, an impression, ×20; 17, ×25 (p. 23). **18,** *Ligonodina* sp. 3. Figured specimen: an impression. ×12 (p. 23). **19, 21,** *Hindeodella aculeata* Huddle. Hypotypes: ×12 (p. 23). **20,** *Hindeodella* sp. 2. Figured specimen: an impression. ×25 (p. 23). **22,** *Hindeodella germana* Holmes. Hypotype: an impression. ×15 (p. 23). **23,** *Hindeodella alternata* Ulrich and Bassler. Hypotype: an impression. ×24 (p. 23). **24,** *Hindeodella* sp. 1. Figured specimen: an impression. ×14 (p. 23). **25,** *Hindeodella subtilis* Ulrich and Bassler. Hypotype: ×20 (p. 23). **26,** *Palmatodella ?* sp. Figured specimen: an impression. ×20 (p. 23). **27,** *Prioniodina separans* Holmes. Hypotype: ×12 (p. 23).

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Systematic Descriptions

Family **Distacodidae** (Ulrich and Bassler, 1926)

The specimens illustrated on Plate I, figures 1–3, represent a small group of distacods recovered from conodont bone bed material by boiling, washing, and screening through the 100-mesh sieve. They are somewhat smaller than many of the distacods described in the literature, but they compare favorably in size with several specimens from Pander's conodont material which was available for comparison. An opaque white appearance is developed more or less completely in these tiny cones, a characteristic which they share with the blade or platform type conodonts recovered with them in the screenings. This opacity conceals the growth axes. The upper parts of the cones have been broken away, but otherwise the luster, striae, and thin edges of the basal cavities are well preserved. Pending the collection and study of additional material no specific nor generic assignments can be made with any assurance at this time.

The illustration on Plate I, figure 1, represents a minute, simple cone having a base which is extended and flared both anteriorly and posteriorly. The basal cavity is moderately large. The cusp is thin, long, curved moderately, slightly compressed laterally, smooth, with a faint keel developed on the anterior edge. (Figured specimen, Ohio State University Geological Museum, no. 18367c.)

Figure 2 on Plate I illustrates a simple cone with a small oval base which is very slightly expanded and has a rather shallow cavity. The cusp is oval in cross-section, smooth, and slightly curved, forming a high angle with the plane of the base. (Figured specimen, Ohio State University Geological Museum, no. 18367a.)

The specimen illustrated on Plate I, figure 3, is a simple cusp with the base slightly but sharply expanded with a broad, shallow basal cavity, and a thin-lipped basal edge. The cusp is laterally compressed, marked with longitudinal striae and a small sharp keel on the anterior edge. It is slightly inclined and curved and thus forms a high angle with the plane of the base. (Figured specimen, Ohio State University Geological Museum, no. 18367b.)

How should the presence of these simple cones in Devonian strata be interpreted? Branson and Mehl (1933b, p. 210) on the basis of their extensive conodont collections, believe that the distacods died out in the Silurian, and Ellison in his recent table showing the stratigraphic ranges of conodonts (1946, p. 94, fig. 1)

EXPLANATION OF PLATE II

All specimens are from the lower portion of the Ohio shale, upper Devonian, central Ohio. Magnification as noted.

Fig. 1, *Metaprioniodus biangulatus* Huddle. Hypotype. ×30 (p. 25). **2,** *Lonchodina perarcuata* Ulrich and Bassler. Hypotype: an impression. ×15 (p. 25). **3,** *Lonchodina multidens* Hibbard. Hypotype: an impression. ×20 (p. 25). **4,** *Lonchodina perlonga* Ulrich and Bassler. Hypotype. ×25 (p. 25). **5,** *Bryantodus concavus* Huddle. Hypotype: an impression. ×30 (p. 25). **6,** *Bryanthodus commutatus* Huddle. Hypotype: ×24 (p. 25). **7, 12,** *Ozarkodina delicatula* (Stauffer and Plummer). Hypotypes: ×30 (p. 25). **8,** *Bryantodus germanus* Holmes. Hypotype: ×24 (p. 25). **9,** *Hibbardella angulata* (Hinde). Hypotype: an impression. ×12 (p. 25). **10,** *Bryantodus inequalis* Holmes. Hypotype: ×18 (p. 25). **11,** *Bryantodus nitidus* Ulrich and Bassler. Hypotype: a restoration based on mold. ×20 (p. 25). **13,** *Subbryantodus radians* Branson and Mehl. Hypotype: ×30 (p. 25). **14,** *Bryantodus serrulus* Huddle. Hypotype: ×25 (p. 25). **15,** *Bryantodus subcarinatus* Huddle. Hypotype: ×20 (p. 25). **16,** *Bryantodus subequalis* Cooper. Hypotype: ×30 (p. 25). **17,** *Bryantodus subplanus* Huddle. Hypotype: ×25 (p. 25). **18,** *Subbryantodus* sp. Figured specimen: ×24 (p. 25). **19,** *Spathognathodus subrectus* (Holmes). Hypotype: ×20 (p. 25). **20,** *Polygnathus* sp. Figured specimen: ×35 (p. 25). **21,** *Polygnathus pennatuloides* Holmes. Hypotype: ×20 (p. 25). **22,** *Polygnathus nodocostata* Branson and Mehl. Hypotype: ×12 (p. 25). **23,** *Polygnathus sublatus* Ulrich and Bassler. Hypotype: ×15 (p. 25). **24, 30,** Dermal plates. Figured specimens: 24, ×12; 30, ×8 (p. 25). **25,** *Palmatolepis glabra* Ulrich and Bassler. Hypotype: ×20 (p. 25). **26,** *Ancyrognathus irregularis* Branson and Mehl. Hypotype: ×12 (p. 25). **27,** *Palmatolepis subperlobata* Branson and Mehl. Hypotype: ×20 (p. 25). **28,** *Palmatolepis quadrantinodosa* Branson and Mehl. Hypotype: ×20 (p. 25). **29,** *Palmatolepis regularis* Cooper. Hypotype: ×12 (p. 25).

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emphasizes their Silurian extinction. These authors state that the numerous references to post-Silurian distacods in the literature are the result of failure to recognize that the cones are the broken-off cusps of Devonian or younger blade and bar types of conodonts or are foreign elements in stratigraphic admixtures. They have discussed many of these mixed faunas in considerable detail (Branson and Mehl, 1940; Ellison, 1946, pp. 100–102).

There is no evidence to suggest that the Ohio shale distacods are an admixture from earlier stratigraphic horizons. The specimens were collected from strata well above the basal contact of the formation, and there is no indication of any intraformational breaks. The distacods have essentially the same color and luster as the typical Devonian genera *Palmatolepis* and *Hindeodella*. The presence of distinct basal cavities and smooth, perfectly defined, unbroken basal margins unquestionably relates them to the family Distacodidae and eliminates *Lonchodina* and *Euprioniodina* assignments such as Branson and Mehl have made for some of their Grassy Creek cone-shaped conodonts (1933b, pp. 210, 211, pl. 15, figs. 15, 21).

The problem resolves itself into a study of three alternatives: 1, the recognition of a stratigraphic admixture; 2, an extension of the range of the distacods beyond the Silurian; 3, separation of these Devonian forms from the family Distacodidae on some basis, however slight, frankly for utilitarian purposes. This last alternative is comparable to the problem of variability of species as commented upon by P. E. Raymond (1941, p. 99), who points out that specimens from zones of different ages are split into different species on the basis of minor characteristics which are considered merely as variations for specimens in the same zone, and notes that this course ". . . by some . . . is carried to such an extreme that the locality seems to be the chief guide to identification."

Further collections and studies are considered necessary before any definite conclusion on this problem can be reached.

Genus **Ancyrognathus** Branson and Mehl, 1933

Ancyrognathus irregularis Branson and Mehl

Plate II, figure 26

Ancyrognathus irregularis Branson and Mehl, 1933, Missouri Univ. Studies, vol. 8, no. 3, p. 242, pl. 19, figs. 1, 2, 4, 10, 16.

Plate broad, irregularly lobate anteriorly, oral surface ornamented with small nodes irregularly arranged, aboral surface with fine concentric lines and a bifurcating keel; carina prominent, composed of fused nodes, bifurcating near center of plate, the branches extending to the ends of the lobes; blade short, heavy, denticulate.

Hypotype, Ohio State University Geological Museum, no. 18417.

Genus **Bryantodus** Ulrich and Bassler, 1926

Bryantodus commutatus Huddle

Plate II, figure 6

Bryantodus commutatus Huddle, 1934, Bull. Am. Paleontology, vol. 21, no. 72, p. 70, pl. 2, figs. 13, 14.

Bar thick, rounded, moderately arched, curved laterally, with a faint keel extending along the entire length of the bar; cusp rather small, in some specimens indistinguishable from adjacent denticle; denticles fused except near tips, somewhat irregular in size, diminishing in length toward the ends of the bar.

Hypotype, Ohio State University Geological Museum, no. 18396.

Bryantodus concavus Huddle

Plate II, figure 5

Bryantodus concavus Huddle, 1934, Bull. Am. Paleontology, vol. 21, No. 72, p. 71, pl. 2, figs. 15–17.

Bar broad, smooth, laterally compressed, strongly arched; cusp long, thick at base, acutely pointed; denticles short, nearly parallel, confluent except at tips, six or eight on each side of cusp.

Hypotype, Ohio State University Geological Museum, no. 18397.

Bryantodus germanus Holmes

Plate II, figure 8

Bryantodus germanus Holmes, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 28, pl. 10, fig. 5.

Bar high, thin, slightly curved laterally but not arched, with a lateral ridge extending along its whole length, aboral edge sharp; cusp short, thick, rounded, inclined slightly; denticles short, close-set but not confluent, twelve anterior to cusp nearly vertical, six posterior to cusp slightly inclined.

Hypotype, Ohio State University Geological Museum, no. 18399.

Bryantodus inequalis Holmes

Plate II, figure 10

Bryantodus inequalis Holmes, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 27, pl. 10, figs. 1, 2. (Not *B. inequalis* Branson and Mehl, 1933, Missouri Univ. Studies, vol. 8, p. 219, pl. 16, figs. 17, 18.)

Bar long, moderately arched, anterior half with prominent median ridge, posterior part thin, slightly curved laterally, aboral edge sharp; cusp short, broad, slightly recurved, inclined; denticles short, sharp-edged, close-set but not fused, ten to fourteen on each side of cusp, the anterior ones being larger and more inclined than those on posterior part of bar.

Remarks.—As noted in the synonymy, the specific name *inequalis* used by Branson and Mehl, was preoccupied by Holmes and a substitute should be proposed. (See Youngquist, 1945, p. 358.)

Hypotype, Ohio State University Geological Museum, no. 18400.

Bryantodus nitidus Ulrich and Bassler

Plate II, figure 11

Bryantodus nitidus Ulrich and Bassler, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 24, pl. 4, figs. 12–14.

Bar heavy, moderately arched, anterior part with prominent median ridge which extends along posterior part as a lateral expansion at base of denticles, aboral edge sharp with a slight expansion beneath cusp; cusp subcentral, rather short, thick, moderately inclined; long, slightly inclined denticles anterior to cusp; rather short, massive, vertical denticles posterior to cusp; all close-set but not confluent.

Hypotype, Ohio State University Geological Museum, no. 18401.

Bryantodus serrulus Huddle

Plate II, figure 14

Bryantodus serrula Huddle, 1934, Bull. Am. Paleontology, vol. 21, no. 72, p. 71, pl. 2, figs. 18–20.

Bar moderately high and thick, slightly arched; cusp inclined, small, only slightly longer and thicker than the denticles; denticles numerous, small, inclined, close-set but not confluent, inserted, a few suppressed denticles present between bases of the developed denticles.

The aboral edges of the specimens observed are imperfectly preserved and therefore do not show characteristics of apical pit or groove.

Hypotype, Ohio State University Geological Museum, no. 18404.

Bryantodus subcarinatus Huddle

Plate II, figure 15

Bryantodus subcarinatus Huddle, 1934, Bull. Am. Paleontology, vol. 21, no. 72, p. 74, pl. 4, figs. 7, 8.

Bar long, thick, moderately arched, posterior part rounded, anterior part with prominent lateral ridge; cusp long, rather thin, inclined; denticles long, thin, straight, appressed but not confluent, seven to ten on each side of cusp, anterior ones vertical, posterior ones inclined.

Hypotype, Ohio State University Geological Museum, no. 18405.

Bryantodus subequalis Cooper

Plate II, figure 16

Bryantodus subequalis Cooper, 1931, Jour. Paleontology, vol. 5, p. 234, pl. 28, fig. 11.

Tooth very small, bar short, rather strongly arched; cusp proportionately large, inclined; denticles small, closely appressed and confluent, deeply inserted, four to six on each side of cusp, those anterior to cusp slightly curved and larger than the posterior denticles.

Hypotype, Ohio State University Geological Museum, no. 18406.

Bryantodus subplanus Huddle

Plate II, figure 17

Bryantodus subplanus Huddle, 1934, Bull. Am. Paleontology, vol. 21, no. 72, p. 73, pl. 4, figs. 5, 6.

Bar thin, slightly arched; cusp long, slightly curved and inclined; denticles long, appressed, deeply inserted, minute suppressed denticles between large ones in central part of bar; anterior denticles large, slightly curved, five or six in number, decreasing in length anteriorly; posterior denticles near cusp thin and short, those near end of bar large.

Hypotype, Ohio State University Geological Museum, no. 18407.

Genus **Euprioniodina** Ulrich and Bassler, 1926

Euprioniodina prona Huddle

Plate I, figures 11, 12

Euprioniodina prona Huddle, 1934, Bull. Am. Paleontology, vol. 21, no. 72, p. 52, pl. 6, fig. 19; pl. 11, fig. 8.

Bar long, somewhat compressed, slightly arched; cusp short, round, thick at base but tapering to a sharp point, inclined strongly forward; anticusp wide, compressed, extending in line with cusp, bearing fine denticles which are close-set and inclined sharply upward; denticles on bar numerous, long, thin, slightly curved and inclined forward, minute denticles set between most of the larger ones.

The species is represented in this collection by clear impressions which closely resemble *Synprioniodina alternata* Ulrich and Bassler (1926, p. 42, text fig. 22 on p. 16). The distinction is made on the basis of the discrete bar denticles which are absent in the genus *Synprioniodina*, and also on the basis of the cusp and anticusp extending in a line as in *Euprioniodina prona*.

Hypotypes, Ohio State University Geological Museum, nos. 18374, 18375.

Genus **Hibbardella** Ulrich and Bassler, 1926

Hibbardella angulata (Hinde)

Plate II, figure 9

Hibbardella angulata (Hinde), 1926, Ulrich and Bassler, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 37, pl. 3, figs. 1–4.

Bar highly arched, limbs moderately heavy, rounded, nearly straight; cusp long, thick, rounded, very slightly curved; denticles rather short, rounded, well separated, slightly curved toward the cusp, four or five on each side of the bar.

Hypotype, Ohio State University Geological Museum, no. 18409.

Genus **Hindeodella** Ulrich and Bassler, 1926

Hindeodella aculeata Huddle

Plate I, figures 19, 21

Hindeodella aculeata Huddle, 1934, Bull. Am. Paleontology, vol. 21, no. 72, p. 40, pl. 4, figs. 19–21; pl. 5, figs. 2, 3.

Bar straight or slightly curved, long, thin, rounded, oral shoulder distinct, anterior portion of bar sharply curved laterally and slightly expanded downward; cusp rounded, curved and inclined posteriorly; denticles inserted, straight, rounded, inclined posteriorly, three or four small denticles between the large ones.

The oral shoulder distinguishes this species from *Hindeodella subtilis* Ulrich and Bassler (1926, p. 39, pl. 8, figs. 17–19).

Hypotypes, Ohio State University Geological Museum, nos. 18383, 18384.

Hindeodella alternata Ulrich and Bassler

Plate I, figure 23

Hindeodella alternata Ulrich and Bassler, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 40, pl. 1, figs. 14, 15.

Bar straight or slightly arched, moderately thick, laterally compressed, anterior portion depressed and curved laterally; cusp long, thick, rounded, curved and inclined backward; several prominent posterior denticles progressively larger and more inclined posteriorly with one to three small denticles set between the larger ones, terminal denticles spine-like; anterior denticles large, slightly curved.

Although the species is represented in the material studied only by impressions, the large cusp and prominent posterior denticles with small denticles set between them are sufficient to identify the species. The form is distinguished from *H. germana* Holmes (1928, p. 25, pl. 9, fig. 9) by the progressive increase in size of the denticles posteriorly. The Ohio shale specimens, like the one from Montana figured by Cooper and Sloss (1943, pl. 29, fig. 18), lack the prominent terminal spine as developed in the cotypes.

Hypotype, Ohio State University Geological Museum, no. 18387.

Hindeodella germana Holmes

Plate I, figure 22

Hindeodella germana Holmes, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 25, pl. 9, fig. 9.

Bar rather short, thick, posterior part straight except for a slight downward deflection at the posterior end where it terminates in a spine-like point, anterior part bent sharply laterally and slightly curved downward; cusp long, slender; denticles ten to fifteen in number, less than half as long as cusp, straight, inclined posteriorly, one or sometimes two minute denticles set between large ones.

Hypotype, Ohio State University Geological Museum, no. 18386.

Hindeodella subtilis Ulrich and Bassler

Plate I, figure 25

Hindeodella subtilis Ulrich and Bassler, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 39, pl. 8, figs. 17–19.

Bar long, rather high and thick; posterior part straight or slightly arched, anterior part deflected downward slightly and curved sharply laterally; cusp long, nearly straight, inclined posteriorly; denticles numerous, small, alternating with three or four minute ones set between the longer ones except for those in front of the cusp which are irregularly arranged.

Hypotype, Ohio State University Geological Museum, no. 18388.

Hindeodella sp. 1

Plate I, figure 24

Bar probably thin, posterior part horizontally straight but slightly bowed laterally, anterior part deflected sharply downward and curved laterally, bearing four to six long denticles with several minute ones in between; cusp long, rounded, slightly curved posteriorly; denticles posterior to the cusp numerous, irregular in size and amount of inclination, generally progressively increasing in size and degree of inclination posteriorly, with fine denticles set between most of the large ones.

This form resembles *Hindeodella deflecta* Hibbard (1927, p. 207, fig. 4c), but the denticles are finer and more numerous than those of *H. deflecta*.

Figured specimen, Ohio State University Geological Museum, no. 18389.

Hindeodella sp. 2

Plate I, figure 20

Bar short, high, compressed, anterior part deflected slightly downward and curved laterally,

posterior part straight, terminating in two short spine-like denticles; cusp prominent, slightly curved and inclined backward; anterior denticles large and slightly curved, posterior denticles rather small with two or three minute denticles set between somewhat larger ones.

This species is represented by two well defined impressions. Its characteristics suggest a new species, but a study of more material is necessary before positive relationships can be determined.

Figured specimen, Ohio State University Geological Museum, no. 18385.

Genus **Hindeodelloides** Huddle, 1934

This genus was established to include forms which differ from *Hindeodella* in the presence of a denticulate anticusp as developed in the genoholotype *Hindeodelloides bicristatus*. Whether this anterior downward projection is an anticusp or merely an excessive bending of the bar is a matter of question which throws doubt on the justifiability of retaining the genus. Ellison (1946, p. 108) suggests the need of additional research before a conclusion can be reached and states that the genus "probably belongs to *Hindeodella* Ulrich and Bassler."

The few specimens observed from the Ohio shale which closely resemble *Hindeodelloides bicristatus* Huddle show an anterior downward deflection and recurving of the bar rather than a development of an anticusp. The evidence is not conclusive, however, and until better material can be studied, it seems best to assign these to the genus *Hindeodelloides*.

Hindeodelloides bicristatus Huddle

Plate I, figures 16, 17

Hindeodelloides bicristatus Huddle, 1934, Bull. Am. Paleontology, p. 48, pl. 7, figs. 2, 3; pl. 12, fig. 6.

Bar short, flattened, rather high, slightly curved, somewhat larger posteriorly than anteriorly; cusp prominent, long, slender, rounded, slightly curved and inclined posteriorly; denticles back of cusp close-set or appressed, straight and inclined posteriorly, minute denticles in between large ones; two or three prominent denticles on posterior part of bar, terminal denticles small; anterior downward projection (anticusp?) large, wide, and slightly recurved, bearing four or five large, up-curved denticles.

The specimens exhibit considerable variation in the length and thickness of the bar, and in the size and inclination of the cusp, but there is prominent similarity with respect to the large, recurved anterior downward projection and the prominent denticles on the posterior part of the bar. The species closely resembles *Hindeodella pumilla* Cooper (1931b, p. 236, pl. 28, fig. 18), but it lacks the long, slightly curved terminal denticle characteristic of that species.

Hypotypes, Ohio State University Geological Museum, nos. 18381, 18382.

Genus **Ligonodina** Ulrich and Bassler, 1926

The fundamental characteristics of the genus *Ligonodina* extend in three dimensions; therefore the features in the two-dimensional laminae surfaces are usually so incomplete that positive specific assignments cannot be made. The impressions described and figured in this paper are the most complete representatives of the dozen or so specimens studied.

Ligonodina sp. 1

Plate I, figure 10

Bar thin, moderately long, slightly curved; cusp long, laterally compressed, slightly curved backward; anticusp short with deep pits in the impression representing four or five denticles which extended from the anticusp at right angles to the plane of the bar and anticusp; bar denticles long, rounded, widely spaced, curved posteriorly, eight to ten in number, with minute denticles set singly between the larger ones on the posterior part of the bar. This form closely resembles *Ligonodina bicincta* Huddle (1934, p. 62, pl. 12, fig. 15).

Figured specimen, Ohio State University Geological Museum, no. 18378.

Ligonodina sp. 2

Plate I, figure 14

Bar short, straight, moderately thick; cusp long, rounded, slightly curved and inclined posteriorly; anticusp rather short, evidence of denticles on anticusp lacking; eight moderately long denticles on the bar with minute denticles set singly between the large ones. The impression shows a close similarity to *Ligonodina gouldi* Cooper (1935, p. 313, pl. 27, fig. 8).

Figured specimen, Ohio State University Geological Museum, no. 18380.

Ligonodina sp. 3

Plate I, figure 18

Bar long, thick, rounded; cusp long, rather thick, rounded, slightly curved posteriorly; anticusp not perfectly represented; bar denticles eight to ten in number, long, rounded, anterior ones apparently rather short, all curved and inclined posteriorly. The impression shows a general resemblance to *Ligonodina falciformis* Ulrich and Bassler (1926, p. 14, pl. 2, figs. 11–13).

Figured specimen, Ohio State University Geological Museum, no. 18379.

Genus **Lonchodina** Ulrich and Bassler, 1926

Lonchodina multidens Hibbard

Plate II, figure 3

Lonchodina multidens Hibbard, 1927, Am. Jour. Sci., 5th ser., vol. 13, p. 203, fig. 3i.

Bar thick, strongly arched, asymmetrical, anterior portion considerably longer than posterior part; cusp short, wide at base, situated near the apex of the arch; denticles curved upward, one or two minute ones set between most of the long ones; one posterior denticle nearly as long as cusp and somewhat more massive.

Hypotype, Ohio State University Geological Museum, no. 18393.

Lonchodina perarcuata Ulrich and Bassler

Plate II, figure 2

Lonchodina perarcuata Ulrich and Bassler, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 33, pl. 5, fig. 19.

Bar strongly arched, rather wide, with a faint lateral ridge; cusp large, rounded, slightly curved, situated at the apex of the arch; denticles quite short, round, anterior ones strongly curved upward, posterior ones almost straight, two of which are nearly equal in size to the cusp.

Hypotype, Ohio State University Geological Museum, no. 18394.

Lonchodina perlonga Ulrich and Bassler

Plate II, figure 4

Lonchodina perlonga Ulrich and Bassler, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 32, pl. 5, figs. 6, 7.

Bar slender, rounded, moderately arched; cusp long, slender, slightly curved; denticles widely separated, long, slender, similar to cusp, four to six on each side of cusp, those anterior to cusp curved, the others straight.

Hypotype, Ohio State University Geological Museum, no. 18395.

Genus **Metaprioniodus** Huddle, 1934

The genus *Metaprioniodus* was established to include forms similar to *Hindeodella* but distinguished by a posterior downward projection. Whether this characteristic is of generic or specific importance is questioned by Ellison (1946, p. 109) who recommends further research and suggests that *Metaprioniodus* probably belongs to *Hindeodella*. Pending further study it seems best to retain the genus *Metaprioniodus* for the two specimens collected from the Ohio shale which resemble very closely Huddle's genoholotype *Metaprioniodus biangulatus*.

Metaprioniodus biangulatus Huddle

Plate II, figure 1

Metaprioniodus biangulatus Huddle, 1934, Bull. Am. Paleontology, vol. 21, no. 72, p. 57, pl. 11, figs. 12, 13.

Bar short, heavy, deflected downward in posterior portion, anterior part deflected downward and curved laterally; cusp large, rounded, curved and inclined posteriorly; several long thin denticles anterior to cusp, back of cusp a number of long and slender denticles alternate with one or two minute ones; three large posterior denticles are sharply inclined backward.

The distinct oral shoulder characteristic of the genoholotype is not developed on the specimens under discussion.

Hypotype, Ohio State University Geological Museum, no. 18391.

Genus **Ozarkodina** Branson and Mehl, 1933

Ozarkodina delicatula (Stauffer and Plummer)

Plate II, figures 7, 12

Ozarkodina delicatula (Stauffer and Plummer) Ellison, 1941, Jour. Paleontology, vol. 15, p. 120, pl. 20, figs. 40–42, 47.

Blade thin, slightly arched, with a slightly flaring lip along aboral edge in some specimens; cusp short but very wide, suppressing adjacent denticles; denticles deeply inserted, appressed, confluent nearly to tips, decreasing in size quite regularly toward ends of blade, nearly vertical at anterior end of blade but progressively more inclined posteriorly.

Hypotypes, Ohio State University Geological Museum, nos. 18398, 18402.

Genus **Palmatodella** Ulrich and Bassler, 1926

Palmatodella delicatula Ulrich and Bassler

Plate I, figure 15

Palmatodella delicatula Ulrich and Bassler, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 41, pl. 10, fig. 5, text fig. 10 on p. 16.

Bar bent anterio-centrally forming a right angle, each limb thin and straight; main denticle or cusp at bend in bar extending nearly in line with posterior limb of bar, posterior denticles small, inserted, closely appressed, strongly inclined forward; anterior denticles long, inserted, closely appressed with a few diminutive suppressed denticles, all at right angles to bar and tapering in length, forming the characteristic palmate structure.

Hypotype, Ohio State University Geological Museum, no. 18377.

Palmatodella ? sp.

Plate I, figure 26

Bar long, straight or slightly arched, probably thin; cusp long, slender, inclined strongly forward, not distinct from denticles below it in some specimens; bar denticles eight or ten in number, vertical, closely appressed, very wide and short, probably bluntly pointed; denticles below cusp long, slender, closely set, extending forward in palmate arrangement usually aligned in the vertical plane with the bar and its denticles.

This species is represented by six clearly defined impressions of such similarity that there is reasonable assurance that the essential characteristics have been preserved. It is similar in its general aspect to *Palmatodella delicatula* Ulrich and Bassler (1926, p. 41, text fig. 20, p. 16), but differs in having very broad, short, vertical denticles on the bar, and in the extension of the palmate denticles from the anterior end of the bar rather than from a downward deflection. The form certainly represents a new species and probably a new genus, but definite relationships cannot be established until better material is collected and studied.

Figured specimen, Ohio State University Geological Museum, no. 18390.

Genus **Palmatolepis** Ulrich and Bassler, 1926

Palmatolepis glabra Ulrich and Bassler

Plate II, figure 25

Palmatolepis glabra Ulrich and Bassler, 1933, Branson and Mehl, Missouri Univ. Studies, vol. 8, no. 3, p. 233, pl. 18, figs. 9, 22, 26.

Plate long and narrow, curved sigmoidally, outline regular except for an abrupt truncation of one side of plate near posterior end, aboral surface marked with fine concentric lines and a thin median keel, oral surface finely pustulose; carina consisting of ten or twelve nodes anterior to the azygous node, and a rather high, thin, node-crested blade increasing in height posteriorly.

Hypotype, Ohio State University Geological Museum, no. 18416.

Palmatolepis quadrantinodosa Branson and Mehl

Plate II, figure 28

Palmatolepis quadrantinodosa Branson and Mehl, 1933, Missouri Univ. Studies, vol. 8, no. 3, p. 235, pl. 18, figs. 3, 17, 20.

Plate broad, subovate in outline, sigmoidally curved, oral surface ornamented with small to moderate-sized tubercles which tend to form rows extending perpendicular to carina; azygous node broadly conical; anterior part of carina straight, consisting of a few small nodes, posterior part curved, crested with small nodes, blade-like posteriorly.

Hypotype, Ohio State University Geological Museum, no. 18419.

Palmatolepis regularis Cooper

Plate II, figure 29

Palmatolepis regularis Cooper, 1931, Jour. Paleontology, vol. 5, p. 242, pl. 28, fig. 36.

Plate sigmoidal in outline, without lobes, pointed at both ends, oral surface minutely granulose, aboral surface almost smooth but showing very faint concentric lines, keel low and sharp; carina sigmoidally curved, crest nodose, probably high and blade-like posteriorly.

Hypotype, Ohio State University Geological Museum, no. 18420.

Palmatolepis subperlobata Branson and Mehl

Plate II, figure 27

Palmatolepis subperlobata Branson and Mehl, 1933, Missouri Univ. Studies, vol. 8, no. 3, p. 235, pl. 18, figs. 11, 12.

Plate thin, broad, with wide lateral lobe, oral surface minutely granulose, aboral surface marked with fine concentric lines and small median keel; azygous node rounded, dome-like; carina back of azygous node is sharp, curved, with a faintly nodose crest, becoming high and blade-like posteriorly; the carina anterior to azygous node is low and faintly nodose; in some specimens a faint ridge branches from the carina and extends through the lateral lobe.

Hypotype, Ohio State University Geological Museum, no. 18418.

Genus **Polygnathus** Hinde, 1879

Polygnathus nodocostata Branson and Mehl

Plate II, figure 22

Polygnathus nodocostata Branson and Mehl, 1933, Missouri Univ. Studies, vol. 8, no. 3, p. 246, pl. 20, figs. 9–13, pl. 21, fig. 15.

Plate subovate, slightly convex on oral side, marked with two or three rows of coalesced tubercles on each side of carina; carina prominent, extending full length of blade, slightly curved, marked with tiny nodes along crest; blade short, thick at base but with sharp crest.

Hypotype, Ohio State University Geological Museum, no. 18413.

Polygnathus pennatuloidea Holmes

Plate II, figure 21

Polygnathus pennatuloidea Holmes, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 32, pl. 11, fig. 14.

Plate subovate, oral surface convex, ornamented with irregularly arranged tubercles and a prominent, wide-based carina, crested with a series of nodes and extending the full length of the plate; blade long and thin. One specimen only, an impression of the oral surface of the plate, has been recognized.

Hypotype, Ohio State University Geological Museum, no. 18414.

Polygnathus sublatus Ulrich and Bassler

Plate II, figure 23

Polygnathus sublatus Ulrich and Bassler, 1926, U. S. Nat. Mus. Proc., vol. 68, art. 12, p. 47, pl. 8, fig. 2.

Plate ovate and somewhat curved, oral surface slightly convex, ornamented with rows of small tubercles arranged in radial rows; carina broad, low, faintly nodose; plate thin, probably long.

The species is represented by a single impression of the oral surface of the plate.

Hypotype, Ohio State University Geological Museum, no. 18415.

Polygnathus sp.

Plate II, figure 20

Plate ovate, slightly curved, somewhat constricted on one side near anterior end; aboral surface marked with fine concentric lines, a sharp median keel, and an escutcheon; oral surface not known; blade long, thin.

Represented by an impression of the aboral side of the plate and therefore lacking sufficient evidence for specific designation.

Figured specimen, Ohio State University Geological Museum, no. 18412.

Genus **Prioniodina** Ulrich and Bassler, 1926

Prioniodina separans Holmes

Plate I, figure 27

Prioniodina separans Holmes, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 27, pl. 9, figs. 16, 17.

Bar long, rounded, moderately arched, posterior part slightly offset laterally at cusp; cusp long, slender, very slightly curved, inclined posteriorly; denticles long, thin, almost straight, widely separated, anterior denticles larger than posterior ones.

Hypotype, Ohio State University Geological Museum, no. 18392.

Genus **Prioniodus** Pander, 1856

Prioniodus alatoides Holmes

Plate I, figures 5, 7

Prioniodus alatoides Holmes, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 24, pl. 9, fig. 3.

Bar straight, narrow, of nearly uniform proportions throughout its length; cusp long, slim, slightly tapered, inclined forward; anticusp short, triangular in outline, distinctly flattened posteriorly, anterior edge essentially in line with anterior edge of cusp; denticles large, long, and tapering, discrete, inclined slightly forward, numbering ten to fourteen. The presence of minute suppressed bar denticles is indicated in some clear impressions as represented in figure 7, Plate I. In the anterior margin of the anticusp small germ denticles are faintly visible in well preserved specimens. They are distinct in weathered specimens and in some impressions.

Hypotypes, Ohio State University Geological Museum, nos. 18369, 18371.

Prioniodus alatoideus Cooper

Plate I, figures 4, 6

Prioniodus alatoideus Cooper, 1931, Jour. Paleontology, vol. 5, p. 232, pl. 28, fig. 1.

Tooth small with thin, flat, straight bar; cusp long, slim, slightly tapered, inclined forward; anticusp short, subtriangular in outline, flattened toward both edges; denticles numerous, long,

slender, inserted and confluent nearly to tips, slightly inclined forward. Minute germ denticles are inserted in anterior edge of anticusp.

The specimens from the Ohio shale compare favorably in size with the holotype and with Cooper's and Sloss's hypotypes (1943, pl. 29, figs. 6, 7, 11), but they are less than half as large as the hypotypes described by Huddle (1934, p. 37, pl. 1, figs. 4, 5) and by Cooper (1939, p. 404, pl. 45, fig. 62; pl. 46, fig. 19). The short, thick bar represented in the fossil impression illustrated in figure 4 is considered a variation within the species. (Cf. Cooper and Sloss, 1943, pl. 29, fig. 6.)

The species is distinguished from *P. alatoides* Holmes (1928, p. 24, pl. 9, fig. 3) on the basis of its numerous, fine, inserted and confluent denticles.

Hypotypes, Ohio State University Geological Museum, nos. 18368, 18370.

Prioniodus alatus Hinde

Plate I, figure 9

Prioniodus ? alatus Hinde, 1879, Geol. Soc. London, Quart. Jour., vol. 35, p. 361, pl. 16, fig. 5.

Bar straight, thick, high, aboral edge sharp; cusp massive, broad, compressed, sharp-edged, inclined forward, projected below bar to form a rather short, triangular anticusp, anterior edge of cusp and anticusp forming a straight line; denticles closely appressed, deeply inserted, free only at tips, regularly decreasing in size posteriorly, a few minute suppressed germ denticles visible between embedded portions of developed denticles.

Hypotype, Ohio State University Geological Museum, no. 18373.

Prioniodus cultratus Ulrich and Bassler

Plate I, figure 8

Prioniodus cultratus Ulrich and Bassler, 1926, U. S. Nat. Mus. Proc. vol. 68, art. 12, p. 9, pl. 9, fig. 7.

Bar short, straight, and rather thin; cusp vertical, long, broad, compressed, sharp-edged; anterior edge straight and posterior edge curved giving the effect of a slight forward inclination; anticusp very small, representing merely an anterior expansion of the bar to meet the slight aboral projection of the anterior edge of the cusp; denticles long, straight, slightly inclined posteriorly, ten or twelve in number, inserted, basal portions closely appressed but upper two-thirds discrete, a few suppressed denticles between developed ones.

The large, broad, compressed, vertical cusp is distinctive of this species. The specimens in the collection studied resemble the specimen figured by Holmes (1928, p. 24, pl. 9, fig. 4) but differ from those figured by Cooper (1931a, p. 146, pl. 20, fig. 2; 1935, pl. 27, fig. 4) in that his fossils show a thin, recurved cusp and curved denticles quite widely separated on the bar.

Hypotype, Ohio State University Geological Museum, no. 18372.

Genus **Spathognathodus** Branson and Mehl, 1941

Genus *Spathodus* Branson and Mehl, 1933, Missouri Univ. Studies, vol. 8, no. 1, p. 46.
Genus *Spathognathodus* Branson and Mehl, 1941, Jour. Paleontology, vol. 15, p. 98.

Spathognathodus subrectus (Holmes)

Plate II, figure 19

Panderodella subrecta Holmes, 1928, U. S. Nat. Mus. Proc., vol. 72, art. 5, p. 31, pl. 10, fig. 15.
Spathodus subrectus (Holmes) Huddle, 1934, Bull. Am. Paleontology, vol. 21, no. 72, p. 91, pl. 7, fig. 17.

Bar high, nearly straight, aboral expansion situated near anterior end; denticles short, confluent except at tips, subequal in size, slightly longer at posterior end of bar than at anterior end.

Hypotype, Ohio State University Geological Museum, no. 18410.

Genus **Subbryantodus** Branson and Mehl, 1933

Subbryantodus radians Branson and Mehl

Plate II, figure 13

Subbryantodus radians Branson and Mehl, 1938, Missouri Univ. Studies, vol. 13, no. 4, p. 141, pl. 34, figs. 22, 23.

Bar short, high, rather thick, moderately arched, aboral edge sharp except for small expansion beneath cusp; cusp short, very wide at base and sharply pointed, thus having a triangular outline; it is inclined and tends to suppress the adjacent posterior denticles; denticles close-set but not confluent, inclined, inserted, posterior ones about half as large as anterior ones, four to six on each side of cusp.

This form is much smaller than the holotype, but the proportionately large cusp, the few denticles, and small aboral expansion below cusp relate it to the species.

Hypotype, Ohio State University Geological Museum, no. 18403.

Subbryantodus sp.

Plate II, figure 18

Tooth small, bar strongly arched, rather high, anterior part thin, straight-sided, laterally straight, posterior part somewhat rounded and curved laterally, apical pit and aboral grooves distinct; apical denticle slightly inclined, short, broad, not sharply distinguished from other large denticles; denticles short, broad, closely appressed, some overlapping, deeply inserted, with minute germ denticles visible deep within bar, small denticles alternating with the large ones on anterior part of bar.

The single specimen of the species in this collection resembles the paratype of *Subbryantodus radians* Branson and Mehl (1938, p. 141, pl. 34, fig. 22), but it lacks the prominent apical denticle characteristic of the species. Additional material is necessary before specific assignment can be made.

Figured specimen, Ohio State University Geological Museum, no. 18408.

Genus **Synprioniodina** Ulrich and Bassler, 1926

Synprioniodina sp.

Plate I, figure 13

Bar short, slightly arched; cusp rather small, flattened, wide at base but tapering rapidly to a sharp point, inclined strongly forward; downward projection of bar (anticusp?) long, broad at base and tapering to a point resulting in a triangular outline; bar denticles fifteen or twenty in number, of medium length, slender, closely set, sharply pointed, curved anteriorly and decreasing in size posteriorly; two or more large denticles closely set in front of cusp, smaller denticles along anterior edge of downward projection, decreasing in size downward, inclined strongly upward.

The few specimens of the species in this collection are impressions, and these indicate distinct features which suggest an undescribed species. However, it is thought best to defer definite assignment until more material can be obtained for study purposes.

Figured specimen, Ohio State University Geological Museum, no. 18376.

DERMAL PLATES

Plate II, figures 24, 30

Black, lustrous plates, rather thin, rhomboid in outline, two margins marked by fine striae which produce a feather-edge effect, surfaces containing small depressions which are elongate longitudinally and irregularly spaced. The plates are of various sizes and dimensions ranging in length from 1.5 to 2.5 mm.

These plates are presumably parts of the protective armour of some type of fish or fish-like animal, but at the present time it is impossible to tie them up with anything definite. Their association with conodonts suggests a morphological relationship.

Figured specimens, Ohio State University Geological Museum, no. 18421.

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AN ECOLOGICAL STUDY OF THE SPIDERS OF A RIVER-TERRACE FOREST IN WESTERN TENNESSEE[1]

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Studies dealing with the ecology of spiders are of two main types: (1) those which give ecological consideration to the entire animal population of the habitat and the spiders incidentally as members of that population, Adams (1915), Weese (1924), Blake (1926), and (2) those which give intensive consideration to the ecology of spiders exclusively of a particular habitat, Elliott (1930), Truman (1942). This study is of the latter nature.

PROCEDURE AND SCOPE OF WORK

Spiders were collected continuously every ten to fourteen days over a period of twenty-two months in a River-Terrace forest located along the secondary terrace of the Wolf river, a tributary of the Mississippi, in the region of Memphis, Tennessee. The land adjacent to the Mississippi River and its tributaries is characterized by typical swamp forest vegetation. As the land rises from the flood plain level, a secondary terrace forest is apparent, composed essentially of an Oak-Gum community along the lowland and Oak-Hickory along the upland, drier portion. Collections were made by beating branches of trees and shrubbery, sweeping herbage, sifting leaves and upper soil layer and removing the bark and wood from trees, stumps and logs. Species were identified by Dr. W. M. Barrows, of the Ohio State University.

THE SPIDER POPULATION OF THE RIVER-TERRACE FOREST

Species inhabiting the forest are listed alphabetically and numbered consecutively in order that they may be referred to by their numerical position in the table which appears below. The names given to the spiders are those, as far as possible, listed in the synonymic Index-Catalogue of Spiders of North, Central and South America (Petrunkevitch).

1. *Acacesia foliata* Hentz.
2. *Agassa cyaena* Hentz.
3. *Agelena americana* Keyserling.
4. *Agelena emertoni* Chamberlin & Ivie.
5. *Agelena naevia* Walckenaer.
6. *Agroeca* sp. ?
7. *Amaurobius americana* Keyserling.
8. *Antistea* sp.?
9. *Anyphaena fraterna* Banks.
10. *Anyphaena saltibunda* Hentz.
11. *Araneus arenatus* Walckenaer.
12. *Araneus benjaminus* Walckenaer.
13. *Araneus marmoreus* Clerck.
14. *Araneus miniatus* Walckenaer.
15. *Araneus stellatus* Walckenaer.
16. *Araneus thaddeus* Hentz.
17. *Araneus tusus* Petrunkevitch.
18. *Arctosa* sp.?
19. *Argiope aurantia* Lucas.
20. *Argiope trifasciata* Forskal.
21. *Argyrodes trigonium* Hentz.
22. *Argyrodes trituberculatus* Becker.
23. *Ariadne bicolor* Hentz.
24. *Aysha gracilis* Hentz.
25. *Bathyphantes micaria* Emerton.
26. *Callilepis imbecilla* Keyserling.
27. *Castaneira longipalpis* Hentz.
28. *Castaneira stupkai* Barrows.
29. *Ceraticelus fissiceps* Cambridge.
30. *Ceraticelus micropalpis* Emerton.

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31. *Ceraticelus minutus* Emerton.
32. *Ceratinopsis* sp.?
33. *Cesonia bilineata* Hentz.
34. *Chiracanthium inclusum* Hentz.
35. *Cicurina itasca* Chamberlin & Ivie.
36. *Clubiona pallens* Hentz.
37. *Crustulina guttata* Wider.
38. *Cyclosa conica* Pallas.
39. *Dendryphantes* (P) *audax* Hentz.
40. *Dendryphantes* (*M*) *capitatus* Hentz.
41. *Dendryphantes insignarius* Koch.
42. *Dendryphantes* (*P*) *whitmanii* Pecham.
43. *Dictyna armata* Banks.
44. *Dictyna bicornis* Emerton.
45. *Dictyna cruciata* Emerton.
46. *Dictyna frondea* Emerton.
47. *Dictyna sublata* Hentz.
48. *Dictyna foliacea* Hentz.
49. *Dictyna zaba* Barrows and Ivie.
50. *Dipoena nigra* Emerton.
51. *Dolomedes* sp.?
52. *Drassodes* sp.?
53. *Drasyllus aprilinus* Banks.
54. *Drasyllus dixinus* Chamberlin.
55. *Drasyllus fallens* Chamberlin.
56. *Drexelia directa* Hentz.
57. *Ebo latithorax* Keyserling.
58. *Epeira juniperi* Emerton.
59. *Erigone autumnalis* Emerton.
60. *Eperigone maculata* Banks.
61. *Ero* (*furcatus?*) Villers.
62. *Euryopis funebris* Hentz.
63. *Eustalia anastera* Walckenaer.
64. *Fuentes lineatus* Koch.
65. *Gea heptagon* Hentz.
66. *Gnaphosa bicolor* Hentz.
67. *Hahnia brunnea* Emerton.
68. *Harbrocestum pulex* Hentz.
69. *Hentzia basilica* McCook.
70. *Herpyllus vasifer* Walckenaer.
71. *Hyctia* sp.?
72. *Kaira alba* Hentz.
73. *Lepthyphantes sabulosa* Keyserling.
74. *Leucage venusta* Walckenaer.
75. *Linyphia communis* Hentz.
76. *Linyphia lineata* Linnaeus.
77. *Litopyllus rupicolens* Chamberlin.
78. *Loxosceles* (*rufescens?*) Dufour.
79. *Lycosa avara* Keyserling.
80. *Lycosa punctulata* Hentz.
81. *Lycosa rabida* Walckenaer.
82. *Maevia vittata* Hentz.
83. *Mangora gibberosa* Hentz.
84. *Mangora placida* Hentz.
85. *Marpissa undata* DeGeer.
86. *Micaria* sp.?
87. *Micrathena gracilis* Walckenaer.
88. *Micrathena reduviana* Walckenaer.
89. *Microneta cornupalpis* Cambridge.
90. *Microneta latidens* Emerton.
91. *Mimetus* sp.?
92. *Misumenops asperatus* Hentz.
93. *Misumenops celer* Hentz.
94. *Misumenops oblongus* Keyserling.
95. *Oedothorax* sp.?
96. *Originates rostratus* Emerton.
97. *Oxyopes aglossus* Chamberlin.
98. *Oxyopes salticus* Hentz.
99. *Pachylomerus* sp.?
100. *Pardosa nigropalpis* Emerton.
101. *Pechamia scorpionea* Hentz.
102. *Pallenes* sp.?
103. *Philodromus minutus* Banks.
104. *Philodromus pernix* Blackwell.
105. *Phlegra fasciata* Hahn.
106. *Phrurolithus alarius* Hentz.
107. *Phrurolithus divinulus* Gertsch.
108. *Phrurolithus dulcineus* Gertsch.
109. *Pirata arenicola* Emerton.
110. *Pirata minutus* Emerton.
111. *Pisaurina mira* Walckenaer.
112. *Sergolius variegatus* Hentz.
113. *Schizocosa crassipes* Walckenaer.
114. *Scoloderus tuberculifer* Cambridge.
115. *Sittious cursor* Barrows.
116. *Synaema parvulum* Hentz.
117. *Tapinopa bilineata* Banks.
118. *Tetragnatha laboriosa* Hentz.
119. *Thanatidius dubius* Hentz.
120. *Theridion differens* Emerton.
121. *Theridion dulcineum* Gertsch & Archer.
122. *Theridion frondeum* Hentz.
123. *Theridion globosum* Hentz.
124. *Theridion kentuckyense* Keyserling.
125. *Theridula opulenta* Walckenaer.
126. *Theridion studiosum* Hentz.
127. *Theridion waliacii* Gertsch & Archer.
128. *Thiodina sylvana* Hentz.
129. *Tmarus* (*angulatus?*) Walckenaer.
130. *Tmeticus* (*asetivalis?*)
131. *Trachelas tranquillas* Hentz.
132. *Uloborus americanus* Walckenaer.
133. *Wala mitrata* Hentz.
134. *Wala palmarium* Hentz.
135. *Xysticus ferox* Hentz.
136. *Xysticus funestus* Keyserling.
137. *Zelotes hentzi M.S.S.* W. M. Barrows
138. *Zygoballus bettini* Pecham.
139. *Zygoballus sexpunctatus* Hentz.

ECOLOGY OF THE RIVER-TERRACE FOREST SPIDERS

A summary of the findings with reference to ecological factors is given below in tabular form. Blank spaces in the table indicate insufficient data for the determination required. The symbols used in the table are as follows:

COLUMN I—Species as indicated by numbers given in the taxonomic listing on pages 38 and 39. A "D" alongside of the number representing the species indicates that the species characteristically inhabits the more moist lowland portion of the forest.

COLUMN II—The number of individuals collected of a particular species.

COLUMN III—Specific relation of the species to the forest. These determinations are based upon a comparative study made between species of spiders inhabiting this forest and those recorded for vegetational associations such as Oak-Hickory, Beech-Maple, Elm-Maple, Wet and Dry Prairie, etc. Also upon numerous collections made along the margins of the forest, the adjacent fields and meadows and other similar forests of the region. Symbols used in column III are:

R—Species typical of the River-Terrace forest.
E—Species usually found along the forest border or in regions where cutting of trees has resulted in a mixed grassland-forest community.
F—Field spiders, those found most often and in greatest numbers in cultivated areas, meadows or grassland.
Fo—Species reported for all forests on which data have been compiled and therefore exhibiting no habitat specificity in this regard.
O—Spiders which though present in the River-Terrace forest are more typical of Oak-Hickory.
Pw—Species characteristically inhabiting the wet prairie.
Pd—Species characteristically inhabiting the dry prairie.
Be—Spiders more typical of Beech-Maple and River-Terrace forest.

COLUMN IV—Characteristic stratal position of the spider population within the forest during the warm part of the year. Symbols used in column IV are:

G—Ground stratum.
H—Herb stratum.
S—Shrub stratum.
A—All strata.
U—Upper strata (herb-shrub-tree).
B—Species found characteristically under or in the crevice of bark.

COLUMN V—Approximate hatching periods for the species. (Suggested periods are good only for the vicinity of Memphis, Tennessee.) The determinations were made by comparing younger and younger stages of various species and by keeping the egg sac of others until hatching occurred. Though the suggested hatching periods are approximations in certain instances, the list is presented in the hope that it will stimulate further investigation on the part of those ecologically minded with resulting verification and necessary correction. Symbols: The months are numbered according to their occurrence in the year.

E—indicates the first half of the month.
M—indicates the mid-portion of the month.
L—indicates the last half of the month.

COLUMN VI—Period during which species matures. Symbols are the same as in Column V.

COLUMN VII—Hibernation stage of the species. In general the determination of the hibernation stage rests upon the mid-winter collection of spiders. Symbols used in Column VII are:

I—spiders that hibernate in immature or adult form.
E—spiders that overwinter in the egg sac as eggs or very young.

TABLE I

I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
1	16	E	H	9E	7L	E	8	2	.....	G?	.....	.....	.....
2D	1	R	G	.....	.....	.....	9	613	R	A	6M	5M	I
3	214	F	A	9E	7M	E	10	237	E	A	6M	5E	I
4	20	F	A	9E	7M	E	11	15	Fo	T	8L	6L	I
5	82	F	A	9E	7M	E	12	18	O	S	8L	6L	I
6	1	.....	H?	.....	.....	.....	13	1	Fo	S	.....	.....	E
7	3	Fo	G	6M	5E	I	14	2	R	S	.....	.....	I

TABLE I—(*Continued*)

I	II	III	IV	V	VI	VII
15	33	F	H	8L	6M	I
16	11	R	T	8L	6L	I
17	8	R	A	8L	6M	I
18	13	.....	G?	.....	.....	I
19	8	E	HS	4L	8L	E
20 D	17	E	U	4M	8L	E
21	3	.....	S	.....	.....	I
22	2	R	S	.....	.....	I
23 S	58	Fo	G	5M	4E	I
24	118	O	A	6M	E5	I
25	7	E	H	.....	.....	I
26	71	E	GH	6M	5E	I
27	6	Fo	G	8L	6L	.....
28	8	R	G	8M	7L	E
29	4	R	H	6M	5E	I
30 D	1	R	G	.....	.....	.....
31	3	Fo	H	6E	4L	I
32?	1	.....	.....	.....	.....	.....
33	3	R	H	8L	6L	I
34	12	R	H	6M	4M	I
35	1	R	G	.....	.....	.....
36	36	Fo	G	6M	5L	I
37 D	1	E	G?	.....	.....	.....
38	3	.....	S	6M	5E	I
39	72	E	U	7E	5L	I
40	18	E	SH	HL	7E	I
41	179	R	A	7E	5L	I
42	51	O	A	.....	.....	I
43	20	R	G	6M	5E	I
44	3	R	G	6M	5E	.....
45	135	R	U	6M	5E	I
46	23	F	H	6M	5E	I
47	11	E	H	6M	5E	I
48	65	E	SH	6M	5E	I
49	177	E	A	6M	5E	I
50	1	.....	.....	.....	.....	.....
51?	1	.....	.....	.....	.....	.....
52	1	.....	.....	.....	.....	.....
53	1	.....	G?	.....	.....	.....
54	2	R	G	6M	5E	I
55 D	24	R	G	6M	5E	I
56	2	Pd	H	.....	.....	I
57	64	R	GH	6E	4L	I
58 D	7	Fo	T	10L	7L	.....
59	6	E	U	4L	9L	I
60	1	.....	G?	.....	.....	.....
61	1	.....	.....	.....	.....	.....
62	5	Fo	U	6M	5E	I
63	23	Fo	HS	8E	5L	I
64	31	E	G	7M	6E	I
65	5	R	H	8M	6L	I
66	2	E	G	.....	.....	.....
67 D	6	R	G	8L	L6	I
68 D	9	E	A	6M	4M	I
69 D	9	R	U	8L	6L	I
70	6	Fo	A	6M	5E	I
71?	1	.....	.....	.....	.....	.....
72	7	R	H	6M	5E	I
73	20	R	G	9L	8E	I
74	80	Fo	U	7L	6L	E
75	40	F	H	6M	5E	I
76	101	F	H	6M	5E	I
77	1	.....	G	.....	.....	.....
78 D	2	R	S	.....	.....	.....
79	157	Rw	G	6E	4E	I
80	2	.....	G	.....	.....	E
81	75	E	GH	9L	7L	E
82	69	E	H	7E	5L	I
83	33	E	H	8L	6L	I
84	86	R	H	7E	6L	I
85	17	O	B	7M	5E	I
86	4	.....	.....	.....	.....	.....
87	1	E	T?	.....	.....	.....
88	2	R	.....	.....	.....	.....
89	4	Be	G	5L	4M	I
90	3	R	G	5L	4M	I
91	15	R	H	.....	.....	I
92	70	Fo	A	6E	5L	I
93	19	R	U	6E	5L	I
94	24	E	U	6E	5L	I
95?	1	.....	.....	.....	.....	.....
96	4	R	TS	.....	.....	I
97	239	R	A	7E	6M	I
98	119	E	H	7L	5M	I
99?	.....	.....	.....	.....	.....	.....
100 D	14	E	G	5M	4L	I
101?	2	F	.....	.....	.....	.....
102	3	.....	.....	.....	.....	.....
103	11	R	T	6M	5E	I
104	39	O	A	6M	5E	I
105	1	R	G	.....	.....	.....
106	143	Fo	G	6M	5E	I
107	4	.....	G	.....	.....	.....
108	1	F	G	.....	.....	.....
109	6	R	G	7E	5L	I
110	16	F	G	7E	5L	I
111	286	E	H	8L	6M	I
112	2	R	H	7E	5M	I
113	57	E	GH	5M	4E	I
114	18	R	U	8L	6L	I
115 D	1	F	.....	.....	.....	.....
116	7	O	GH	5M	8M	I
117	2	.....	A	.....	.....	.....
118	121	E	H	7E	6M	I
119	115	R	A	7E	5L	I
120	22	E	U	6E	5E	I
121 D	1	R?	.....	.....	.....	.....
122	5	E	H	.....	.....	.....
123	42	R	H	6M	5E	I
124	4	R	T	.....	.....	.....
125	33	E	A	8E	7M	I
126 D	63	R	T	7E	6M	E
127	2	.....	G	.....	.....	.....
128	90	R	A	7E	5E	I
129	3	.....	.....	.....	.....	.....
130	3	.....	G	.....	.....	.....
131	4	E	.....	8L	6L	I
132	49	Fo	H	9L	8E	I
133	8	R	S	6M	5M	I
134	2	O	T	.....	.....	I
135	31	E	GH	6M	4L	I
136	33	E	GH	6L	4L	I
137	6	E	G	8L	6L	I
138	1	R	H	.....	.....	I
139	28	R	H	6L	4L	I

THE HABITAT

The River-Terrace forest, like the Deciduous forest in general, presents well defined strata. These are forest floor, herb layer, shrub layer and forest crown. Because of the influence of the forest crown and the absence of conditions such as exist in associations like arctic tundra and desert, environmental conditions are more uniform. Habitat situations within the forest, as pertaining to spiders, primarily reflect differences associated with the various vegetational strata from forest floor to forest crown. It is axiomatic that soil temperatures in general and especially forest soil temperatures are more stable than the overlying atmospheric temperature. Periodic checks of temperature, light and humidity in the strata of the forest under investigation substantiated the observations made by Weese, Blake and others that the forest floor has the lowest temperature of the strata generally during the summer, and highest during the winter. Humidity is greatest and light intensity lowest at the forest floor. The rate of evaporation was not checked, but it may be assumed that the evaporation rate is least at the ground-leaf layer. Weese (1924) has given proof of this for the Elm-Maple forest which he investigated. From the forest floor upward light intensity, temperature and evaporation increases while humidity decreases. Fluctuations in these physical factors of the environment occurs least in the ground-leaf layer and most in the forest crown, the reasons for this have been fully explained by Adams (1915), Weese (1924) and Blake (1926).

Spiders inhabiting the ground-leaf layer are species tolerant of little light, comparatively low temperature, a fair degree of moisture and low evaporation. The population of this stratum is the most constant of all the strata except during the winter months when migrants characteristic of other situations hibernate in it. This constancy of population is associated with physical factor gradients which exist between the ground-leaf layer and the adjacent herb layer. Spiders passing from one of these strata to the other undergo marked and sometimes very sharp changes.

Similar differences exist with regards to herb, shrub and tree strata but the gradients are not as steep nor as controlling in their effect.

The transitional nature of the forest under investigation affords a more varied habitat than more homogeneous vegetational associations such as Oak-Hickory or Beech-Maple forests because the River-Terrace Forest gradually changes from the more dense humid and shady forest of the lowland to the drier, more open Oak-Hickory association of the upland. Also, the presence of prairie vegetation in certain regions of the area adds further to the diversified nature of the habitat. Correlated with these varied biotic and physical features, there is much diversification in the spider population.

DISCUSSION

The stratal and habitat relations given above are not intended to indicate that the spiders are limited to the designated situations, but that the particular species are found most often and in greatest numbers in the micro-habitat or habitat suggested. Some of the spiders are apparently tolerant of a wide variety of conditions and can be found virtually in all situations in substantial numbers. Comparative abundance alone cannot be used as a criterion for determining habitat preferences, as the table shows, it often happens that a species characteristic of one habitat is numerically dominant in another; for example, *Agelena naevia*—a field form—and *Pisaurina mira*—a transitional form—are among the most numerous in the River-Terrace forest.

Physical factors are the dominant forces in the activities of the spiders during the winter. The habitat is essentially reduced to a single layer, the ground-leaf stratum. In southern Tennessee, however, a few species can be collected from

the remnant herb layer throughout the winter. As pointed out by Weese (1924), preceding hibernation there is a general downward migration of the spiders but certain species such as *Clubiona pallens* and *Ariadna bicolor* move upward with the advent of winter and hibernate under the bark of trees. Activity is reduced to a minimum during hibernation except on warm days when certain species move about on the dead leaves and herbs but even then evidence of predatory activity is lacking.

The mass hatchings indicated in the table during the late spring and the late summer result in two population peaks in the population density of the spiders when the young hatched at these periods mature. The fact that the hatching period and time of maturity of the species given above are somewhat earlier than published reports in this regard for the same species farther north, and that species reported as overwintering as eggs or egg-sized spiders in the north are readily collected from one-fourth to one-half grown in the Memphis area indicate the effect of environment on the reproductive and developmental processes of the spiders.

SPECIES DIAGNOSTIC OF THE HABITAT

Only thirty species were represented by fifty individuals or more in the collections. The total number of individuals of these thirty species constitute more than three-fourths of the 5,090 spiders taken. Among these principal or numerically dominant groups were some more typical of other habitats as the table shows. However, it is interesting to note that certain of these principal species occur in great abundance in this forest while being very scarce or absent in other vegetational communities studied. Further, according to published reports and information gained from collectors, one of the species (*Oxyopes aglossus*) though widely distributed, seems to be found in large numbers only in this type of habitat. Species of this nature are: *Oxyopes aglossus*, *Anyphaena fraterna*, *Thiodina sylvana*, *Mangora placida*, *Dictyna cruciata*, *Theridion studiosum* and *Ebo latithorax*. Collectively, they are diagnostic of the River-Terrace forest.

SUMMARY AND CONCLUSION

Although a great variety of species inhabit the forest, a comparatively few species make up the largest part of the total number of individuals collected. One hundred and thirty-nine species of spiders are reported for the forest. Thirty species, or approximately one-fifth of the total number, constitute 4,007 individuals or over three-fourths of the 5,090 individuals collected.

Principal species numerically are not always spiders typical of the forest, but may be forms more characteristic of other situations such as the forest border or field.

Of the spiders whose habitat relations were determined, 46 were typical River-Terrace forest spiders; 24 were forest spiders but more typical of other forests (Beech-Maple, Oak-Hickory, Elm-Ash-Maple, etc.); 33 were transitional forms and 11 were field spiders.

Seven species which we consider particularly diagnostic of the River-Terrace forest have been listed.

During the warm part of the year vertical distribution of the species is characterized by stratal communities. Stratification is associated with the physical factors and the vegetation.

Species composition of the stratal communities is not constant but shows seasonal variation.

Horizontal distribution is largely associated with varying moisture content of the soil.

Most of the spiders hibernate as immature forms or adults. Only 14% of the spiders whose hibernation stage was determined overwinter as eggs or egg-size spiders.

Over 90% of the species hibernate in the ground-leaf stratum, thus preceding hibernation there is a general downward migration. Apparently temperature is the chief factor affecting this vertical shifting.

The spiders exhibit two major hatching periods, late spring and late summer.

The mass hatchings of late spring and late summer result in two population peaks of adults when the spiders hatched at these times have matured.

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SOME NEW SPECIES OF IDIOCERUS (HOMOPTERA—CICADELLIDAE) FROM THE UPPER MISSISSIPPI VALLEY

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The species of Idiocerus have been distinguished primarily upon the basis of color markings. Some significance has been given to the size and type of antennal discs which are differential in the males. In view of the use of color characteristics it is apparent that two or more species which have no color markings or which are very similarly marked have been included under a single name. During the past few years the genital structures of the males have been used to separate these similar forms into species but it has been necessary to determine or select the species already described. Through the assistance and cooperation of Dr. Paul Oman, Curator of Hemiptera, U. S. Nat. Musuem, lectotypes have now been selected from the type series and specific morphological characters have been established for I. *pallidus*, *nervatus*, *alternatus* and *lachrymalis*. Illustrations of these characters will be published in a subsequent article.

In order that the names of six of these new species previously placed under the names mentioned above may be used in a completed manuscript covering the faunal study of a geographic area it seems advisable to describe this limited group of species at the present time and illustrate the characters by which they may be recognized.

Idiocerus telus n. sp.

Resembling *pallidus* in form and appearance but with different male genitalia. Length, 5 mm.

White tinged with green without dark markings, basal angles of scutellum yellowish. Elytra subhyaline, veins tinted with green. Face pale. Antennal discs large, black, ovate.

Genitalia: Male plates elongate, rather narrow. Styles slightly broadened near apex,then rapidly narrowed to a pointed apex. Each style bears a prominent spine just before apex. Ventral portion of aedeagus tapered from base to apical fifth which is broadened by a pair of prominent spines which are "webbed" to the main aedeagus shaft. These spines slope almost to apex giving the head portion a triangular appearance, with a blunt apex. The dorsal portion is shorter and constricted at middle between a rather broad base and a broader, diamond shaped apex. The latter has a pointed apical margin, and a broadened pointed lateral margin on each side.

Holotype male and paratype male collected at Pike, Ill., June 28, 1934, by DeLong and Ross.

Holotype in Illinois Natural History Survey Collection.

Idiocerus incomptus n. sp.

Resembling *nervatus* in form and coloration but with distinct male gentalia. Length 4.5 mm

Color pale green to yellow green without markings except pale brownish spots on basal angles of scutellum. Elytra subhyaline with pale veins. Dark veins of under wings conspicuous from above. Face pale, slightly infuscated above.

Antennal discs slightly enlarged, elongate, black at apex.

Genitalia: Male plates elongate, rather narrow, apices broadly rounded. The styles are rather narrow and are tapered about two thirds of their length to form pointed apices each of which bears a large spine. The ventral portion of the aedeagus is only slightly narrowed from base to apex, the latter of which is rounded and bears a short spine either side about one fifth the distance from the apex. The dorsal portion of the aedeagus is constricted at the middle forming a rounded portion at the base which is distinctly wider than the ventral process and a

smaller rounded portion just slightly wider than the ventral process at the apex; this terminates just anterior to the spines of the ventral process.

Holotype male collected from cypress at Horseshoe Lake, Illinois, July 11, 1935, by DeLong and Ross.

Holotype in Illinois Natural History Survey Collection.

Idiocerus apertus n. sp.

Form and general appearance of *nervatus* but pale brownish in color. Length male 4.5 mm.

Vertex broadly rounded, a little shorter at middle than next the eyes. Color, yellowish tinted with brown. The central portion of vertex brownish. Disc of pronotum, basal angles of scutellum, and basal portion of elytra tinted with brown. Elytra subhyaline with pale brownish veins.

Genitalia: Male plates elongate, rather narrow, apices broadly rounded. Styles strongly curved outwardly, apex bluntly pointed and bearing a pair of conspicuous spines. Aedeagus with the ventral portion forming a slightly enlarged apical head with a barbed spine at the base on either side; the dorsal portion is not quite as long as the ventral and is broadened at the apex to form a pointed protrusion at either side and a broad, slightly produced apical margin.

Holotype male collected at Covington, Tenn., June 18, 1915.

Holotype in the collection of the senior author.

Idiocerus apache var **juniperus** n. var.

Resembling *alternatus* in form and general appearance but with larger antennal discs and distinct genitalia. Length 4.5–5mm.

Face pale, lorae and genae with heavy brown longitudinal stripes. Upper portion of face with a large median dark area which extends across vertex as in *alternatus*. Vertex pale brown with a round black spot each side not far from eye and just above margin. Pronotum pale brown tinted with gray and with dark brown markings on anterior portion. Scutellum cream to pale brown, black spots in basal angles and a broad longitudinal white stripe on apical half. Elytra brownish subhyaline, veins dark brown interrupted by white portion at middle of clavus and apex of clavus. Male antennal discs black, elongate, ovate.

Genitalia: Female last ventral segment scarcely produced posteriorly, almost truncate Male plates elongate, rather narrow. Styles tapered, apical half rather slender, bearing a pair of spines near apex on dorsal portion. Ventral portion of aedeagus rather straight and slender with a pair of short barb like spines a short distance from apex. Dorsal portion of aedeagus broadened gradually then abruptly to form a broad apex which is slightly trilobate on apical margin and forms broad pointed lateral processes.

Holotype male taken at Mahomet, Ill., April 30, 1936, Frison and Ross. Allotype female from Golconda, Ill., June 22,1932 (Ross, Dozier and Park). Paratype males and females collected at Golconda, Ill., Urbana, Ill., April 6, 1900; Horseshoe Lake, Ill., July 11, 1935, by DeLong and Ross. Also Kampville, Ill., June 27, 1934, by DeLong and Ross.

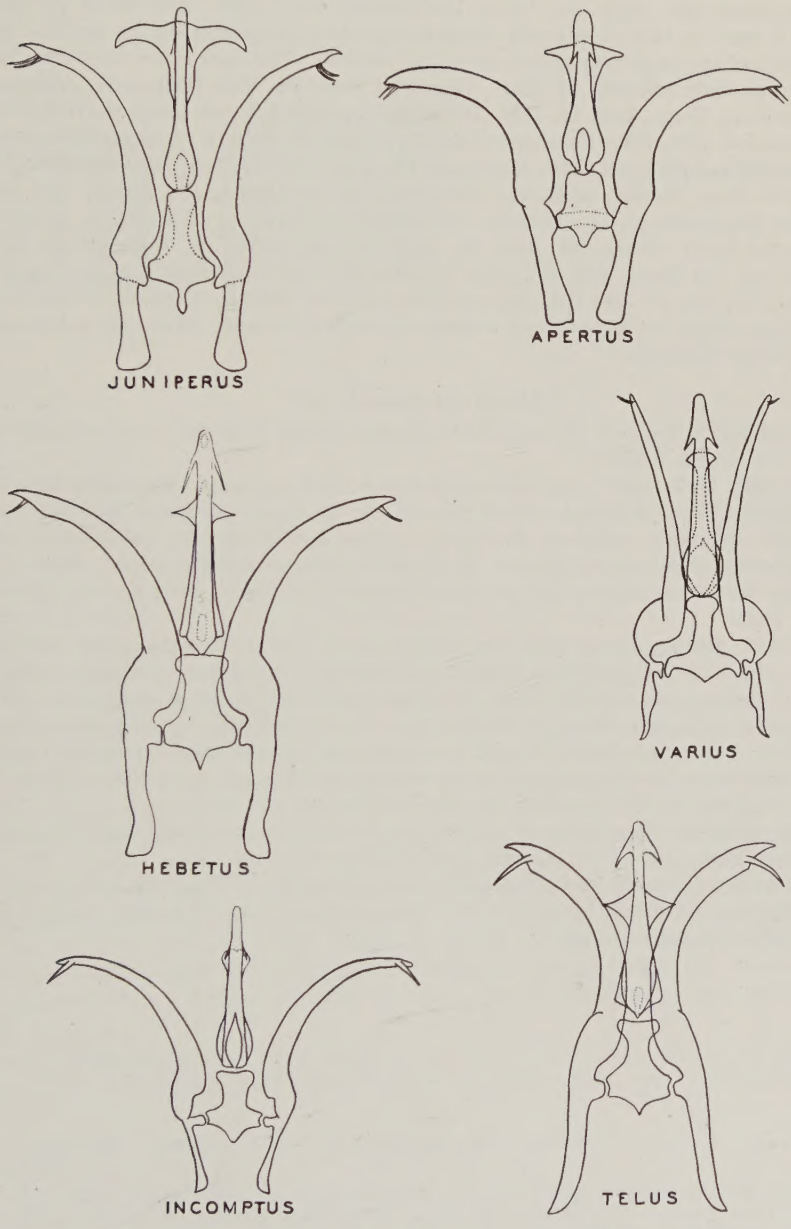
Holotype, allotype and paratypes in Illinois Natural History Survey Collection. Paratypes in senior author's collection.

This species was in manuscript before the recent publication of the species in the Ball collection. In view of its similarity to *apache* Ball and Parker, it is being placed as a variety of that species until further comparison can be made with the type.

Idiocerus varius n. sp.

Resembling *alternatus* in general coloration and apppearance but with distinct male genitalia, and large antennal discs. Length 5–5.5 mm.

Face marked as in *alternatus* with a large median dark area on upper portion extending across vertex. The vertex is marked with an elongated brown spot next each eye and a large round black spot not far from each eye just above margin. Pronotum brown with heavy dark markings. Scutellum pale brown with black spots in basal angles and a series of small connected black spots across middle. Elytra pale brownish subhyaline, veins dark brown interrupted by white veins at the middle of clavus and across elytron at apex of clavus. Male antennal discs broad, ovate and black.



Ventral views of aedeagi and styles of species of Idiocerus as labeled.

Genitalia: Female last ventral segment slightly roundedly produced posteriorly. Male plates elongate and narrow. Styles long and slender with a spine on each near apex. Ventral portion of aedeagus rather broad at base and tapered to form a rather narrowed head with a barb-like spine either side about one fourth the distance from apex. The dorsal portion of the aedeagus is broad at base, constricted on median portion and narrow to apex which is broadened to the width of the projecting spines on ventral portion. The apex is convexly rounded.

Holotype male collected at Paris, Tennessee, June 16, 1915 (DeLong). Allotype female from Dyersburg, Tenn., June 17, 1915 (DeLong). Male and female paratypes from Clarksville, Tenn., June and July, 1915; Cranberry Lake, N. Y., July 8, 1920 (R. J. Sim); Jemez Springs, N. Mex., June 16 and Sept. 15, 1919; Algonquin, Ill., July 1895 and July 1896; Golconda, Ill., June 22, 1932, by Ross, Dozier and Park; Castle Rock, Grand Detour, Ill., July 2, 1932, by Dozier and Mohr; Shawneetown, Ill., June 14, 1934 (DeLong and Ross); Karnak, Ill., June 14, 1934 (DeLong and Ross); Vienna, Ill., June 14, 1934 (DeLong and Ross); Rock Island, Ill., July 7, 1934 (DeLong and Ross); Jeff, Ill., June 12, 1934 (DeLong and Ross); Apple River Canyon State Park, Ill., July 11, 1934 (DeLong and Ross); July 16, 1936, by Mohr.

Holotype, allotype and paratypes in senior author's collection. Paratypes in Illinois Natural History Survey Collection.

Idiocerus hebetus n. sp.

Resembling lachrymalis in form and appearance but paler in color and male genitalia different. Length 6–7 mm.

Face pale, ocelli dark. A broken dark brown band on margin forming a dark spot next each eye, and a band produced upward on each end to include the round spot which occurs on *lachrymalis*. Pronotum cream to dark gray, median anterior portion pale brown. Scutellum white to cream, basal angles brown. A transverse line at middle brown. Elytra brownish subhyaline, darker on anterior half of clavus and apical portion. Male antennal discs narrow, elongate, black.

Genitalia: Male plates elongate and rather narrow. The styles are rather broad and only slightly tapered to near apex then pointed and bearing a prominent spine near apex. Ventral portion of aedeagus stout with a pair of rather long basally directed spines just before apex. Dorsal portion of aedeagus broader at base than ventral portion, narrowed, then broadened at apex to form a diamond shaped tip with a pointed apex and the lateral margins sharply angled.

Holotype male, allotype female and male and female paratypes collected from Aspen at Galena, Ill., June 28, 1935 and July 16, 1934, by DeLong and Ross.

Holotype male, allotype female and male and female paratypes in Illinois Natural History Survey Collection. Paratypes in senior author's collection.

This species can easily be distinguished from *lachrymalis* by the paler, more uniform, color; the smaller diamond shaped terminus of the dorsal aedeagus; and the single instead of the double spines at the apices of the styles.